Wetlands (2019) 39:645–684
https://doi.org/10.1007/s13157-019-01174-7

MARK BRINSON REVIEW

Typha (Cattail) Invasion in North American Wetlands: Biology, Regional Problems, Impacts, Ecosystem Services, and Management

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Received: 28 January 2019 / Accepted: 14 May 2019 / Published online: 21 June 2019

Abstract

Typha is an iconic wetland plant found worldwide. Hybridization and anthropogenic disturbances have resulted in large increases in *Typha* abundance in wetland ecosystems throughout North America at a cost to native floral and faunal biodiversity. As demonstrated by three regional case studies, *Typha* is capable of rapidly colonizing habitats and forming monodominant vegetation stands due to traits such as robust size, rapid growth rate, and rhizomatic expansion. Increased nutrient inputs into wetlands and altered hydrologic regimes are among the principal anthropogenic drivers of *Typha* invasion. *Typha* is associated with a wide range of negative ecological impacts to wetland and agricultural systems, but also is linked with a variety of ecosystem services such as bioremediation and provisioning of biomass, as well as an assortment of traditional cultural uses. Numerous physical, chemical, and hydrologic control methods are used to manage invasive *Typha*, but results are inconsistent and multiple methods and repeated treatments often are required. While this review focuses on invasive *Typha* in North America, the literature cited comes from research on *Typha* and other invasive species from around the world. As such, many of the underlying concepts in this review are relevant to invasive species in other wetland ecosystems worldwide.

Keywords Everglades · Hybrid vigor · Hydrology · Invasive species · Laurentian Great Lakes · Nutrient enrichment · Prairie pothole region · *Typha angustifolia* · *Typha domingensis* · *Typha* × *glauca* · *Typha latifolia*

Introduction

Typha (commonly referred to as 'cattail') is the only genus in the family Typhaceae. This iconic genus, comprised of nearly 40 species and hybrids, is ubiquitous across wetland ecosystems throughout the world. An abundance of wind-dispersed seeds allows *Typha* to colonize wetlands across great distances, and its rapid growth rate, large stature, and aggressive clonal propagation can result in dense monotypic stands. These stands have considerable impact on local fauna and flora, biogeochemical cycling, and wetland hydrology, which correspondingly impact wetland functions. Over recent decades, the distribution and abundance of *Typha* in wetland ecosystems around the world, particularly in North America, has increased due to anthropogenic-related disturbances to wetland hydrology and nutrient loads. In addition, vigorous non-native and hybrid taxa have exacerbated the rapid spread of *Typha*. The invasion and expansion of *Typha* in wetland ecosystems have required widespread management, albeit control is often short-lived or ineffective. Despite the negative impacts of *Typha* on natural systems, this plant can provide beneficial ecosystem services under certain conditions, including bioremediation in constructed wetlands to reduce nutrient loads and pollution, and providing biofuel feedstocks needed to help offset global carbon dioxide (CO_2) emissions. In this paper, we conduct a robust, systematic review and

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synthesis of *Typha* across a number of topics, taxa, and regions to address the many issues surrounding *Typha* in North America; many of the underlying concepts in this review are also relevant to invasive species in other wetland ecosystems worldwide.

The designation of *Typha* as 'invasive' is subjectively applied and not clear-cut. North America has three dominant species of *Typha*: *T. latifolia* L. (broadleaf cattail), *T. angustifolia* L. (narrowleaf cattail), and *T. domingensis* Persoon (southern cattail), as well as a hybrid taxon *T.* × *glauca* Godr. (cross of *T. latifolia* and *T. angustifolia*) (Smith 2000). *Typha latifolia* and *T. domingensis* are native to North America, *T. angustifolia* is likely not native with European origins, and *T.* × *glauca* is a hybrid. The term 'invasive' is usually associated with non-native species but can also be applied to native species that increase in abundance in response to environmental change and dominate wetlands by displacing other species. For example, nutrient enrichment from agricultural runoff led to a considerable increase in native *T. domingensis* abundance in the southern US, and changes in hydrologic regimes facilitated the proliferation of non-native *T. angustifolia* and hybrid *T.* × *glauca* in the northern US/southern Canada. Thus, the term 'invasive' is context-dependent and can be associated with native, non-native, and hybrid taxa of *Typha*.

Section 1: Biology and Ecology of *Typha*

Distribution

Typha is found worldwide on every continent except Antarctica (Smith 1987) (Fig. 1). *Typha* is an ancient genus with its origins dating back at least to the mid-Eocene (39 Mya) in eastern Eurasia (Zhou et al. 2018). From there, *Typha* diversified and dispersed around the world, including to North America via the North Atlantic Land Bridge and Beringian Land Bridge migration routes. Of the four dominant taxa found in North America, *T. latifolia* is the widest ranging, extending throughout virtually the entire continent. This species is found in the broadest climatic conditions of all *Typha*, persisting as far north as boreal-arctic transition zones in Northwest and Yukon Territories and Alaska, where mean winter temperatures reach −20 °C, and as far south as the subtropical zone of the southern US, where average summer temperatures exceed 27 °C (Smith 1967; Grace and Harrison 1986; Smith 2000). *Typha angustifolia* is not as tolerant of harsh winter temperatures as *T. latifolia*, and historically had a narrower distribution; it was confined to the eastern seaboard based on pollen and herbarium records (Shih and Finkelstein 2008), but currently ranges across the Great Lakes region to the Mississippi River, southern Manitoba, and has been recorded in scattered populations in the western US and in the boreal transition zone of northern Ontario, Canada (Smith 2000; Shih and Finkelstein 2008). While *T. angustifolia* is possibly native to the tidal wetlands of the eastern seaboard (Shih and Finkelstein 2008), pollen studies have shown that with land use changes such as increased sediment and nutrient influxes to estuarine habitats, there can be substantial increases in local abundances of all *Typha* species (Hilgartner and Brush 2006). *Typha angustifolia* is largely absent from the southern US, but whether this is due to physiological limitation or ecological competition is not known. Due to difficulties in visual identification of *T.* × *glauca*, its range is uncertain; it is likely found where its parental species *T. latifolia* and *T. angustifolia* co-occur (Travis et al. 2010; Freeland et al. 2013). *Typha domingensis* is a warm temperate and pantropical species found in the southern US, primarily Florida and other Gulf states, including Alabama, Louisiana, Mississippi, and Texas. However, scattered populations of *T. domingensis* have been observed as far north as Delaware (Smith 2000). There are few studies on climatic controls of *Typha* life history traits and their roles in setting range limits. In one example, Ekstam and Forseby (1999) documented temperature requirements for germination, with optimal germination rates occurring around 20 °C for *T. latifolia*, although germination can occur across a wide range of temperatures and diurnal amplitudes. By contrast, when grown on its typical peat substrate, *T. domingensis,* had its highest germination percentage and shortest germination period at higher temperatures (83–85% and 1.1–2.5 days at 30 °C) compared to lower temperatures (0–5% and 8.1–19.4 days at 15 °C) (Lorenzen et al. 2000). Thus, while limited, there is some support for the role of climate in controlling species distributions.

Typha latifolia, *T. angustifolia*, and *T.* × *glauca* can generally be identified to species in pollen records (Finkelstein 2003); therefore, dated sediment cores in which pollen is preserved are a means to track invasion history over time. Plant collections housed in herbaria are another method of tracking temporal changes in distributions. An analysis of >1100 herbarium records and of available pollen records archived publicly in the North American Pollen Database confirmed that *T. latifolia*, *T. angustifolia*, and *T.* × *glauca* have all been increasing in abundance since the onset of the settlement period in North America (Shih and Finkelstein 2008). Prior to 1930, *T. angustifolia*, in particular, spread from a restricted range along the east coast of the US westward into the Great Lakes region and the St. Lawrence Seaway; this spread likely occurred in response to anthropogenic land-use change, increased runoff and sedimentation, and enhanced propagule pressure as European settlers converted land to agricultural uses, as well as through the commercial nursery trade (Galatowitsch et al. 1999; Shih and Finkelstein 2008; Rippke et al. 2010; Sritrairat et al. 2012; Ciotir et al. 2013; Ciotir and Freeland 2016; Ciotir et al. 2017; Boxem et al. 2018). Concurrently, the hybrid *T.* × *glauca* appeared in

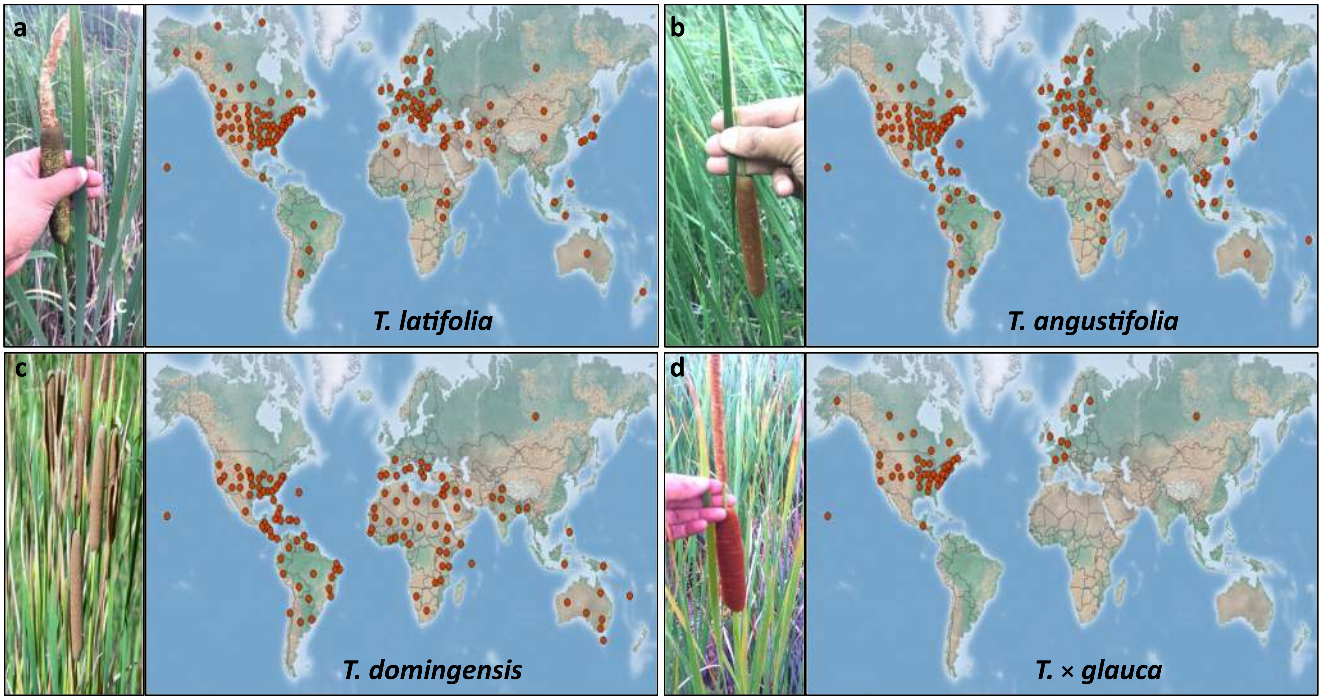

Fig. 1 Example photos of dominant *Typha* taxa in North America and locations (red dots) where **a** *T. latifolia*, **b** *T. angustifolia*, **c** *T. domingensis* and **d** *T.* × *glauca* have been identified. Photos show differences in leaf widths and gap lengths between male (upper yellow) and female (lower brown) regions of the inflorescence among the taxa. Distribution maps modified from (CABI 2018a, b, c, d)

herbarium and pollen records in areas where the ranges of *T. latifolia* and *T. angustifolia* began to overlap (Shih and Finkelstein 2008). Aerial photo analyses have been used to verify independently the accuracy of sediment core pollen records for tracking the time series of *Typha* invasion; Lishawa et al. (2013) combined these approaches to produce high-resolution reconstructions of invasion dynamics for *T. angustifolia* and *T.* × *glauca* in Great Lakes coastal wetlands. Assessing invasion dynamics of *T. domingensis* is difficult because it is often confused with other species, particularly *T. angustifolia* (CABI 2018d; Wunderlin et al. 2018).

Life History and Adaptive Morphological Traits

Rapid Growth and Morphology

Typha dominance in wetlands is largely attributable to its large stature at maturity combined with rapid clonal expansion (Lishawa et al. 2010; Travis et al. 2011; Larkin et al. 2012a, b) (Fig. 2a). Width of the long, linear leaves varies among species; *Typha latifolia* has the widest leaves and *T. angustifolia* has the narrowest, while *T.* × *glauca* and *T. domingensis* have intermediate-width leaves (Grace and Wetzel 1981; Snow et al. 2010; Kirk et al. 2011) (Fig. 1). *Typha* growth rates are relatively high compared to other species, with a maximum of 30–40 g m^{-2} day^{-1}, for an annual total of 10–30 tons ha^{-1} $yr.^{-1}$ (Andrews and Pratt 1978; Dubbe et al. 1988; Miller and Fujii 2010; Grosshans 2014). Rapid growth in spring is fueled by stored carbohydrates (*see rhizomes*, Fig. 2c). *Typha* tends to be more responsive to environmental change than competitors, making it more adaptable to disturbed environments (Newman et al. 1996; Li et al. 2010; Webb and Zhang 2013). *Typha* also displays rapid nutrient uptake in nutrient-rich environments (Newman et al. 1996; Miao and Sklar 1998; Cicek et al. 2006).

Air-Ventilation System

The ability to supply belowground rhizomes and roots with oxygen (O_2) through a system of aerenchyma or intercellular air spaces is a key adaptation of wetland plants (Armstrong 1979; Armstrong et al. 1992) (Fig. 2b). *Typha* uses a pressurized gas flow system, in which O_2 enters through stomata on younger leaves into a high-humidity intercellular atmosphere, then convects along a humidity gradient from leaves to rhizomes and roots and eventually out through older, dead or damaged leaves to the much drier, ambient atmosphere (Chanton et al. 1993; Bendix et al. 1994; Tornberg et al. 1994; Sorrell et al. 2000) (Fig. 2b). Gas flow may be enhanced by pressure developed from wind blowing across dead and broken stems, which have been shown to aerate rhizomes (Jordan and Whigham 1988; Armstrong et al. 1992). The high efficiency of the *Typha* root-aeration system helps give it a competitive advantage over other species, especially in organic-rich, flooded soils (McKee et al. 1989). For example, in the Everglades, *T. domingensis* was shown to have greater O_2

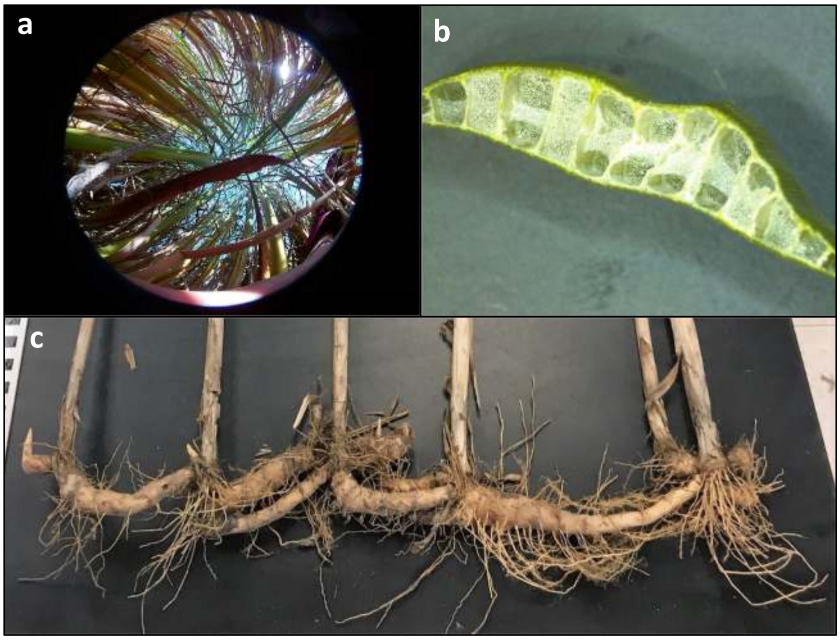

Fig. 2 *Typha* has a number of adaptive traits that allow it to grow and thrive in wetland environments: **a** dense stands of *Typha* inhibit growth of competing vegetation; image is a hemispherical photo from the point of view of an emerging seedling in a *Typha* stand, **b** a *Typha* leaf cross-section shows aerenchyma that allows *Typha* to transport oxygen to roots efficiently, and **c** rhizomes and roots of *Typha*; rhizomes allow *Typha* to propagate clonally and store carbohydrates for regrowth in spring

supply to roots than other native competitors like *Cladium jamaicense* (saw-grass) (Chabbi et al. 2000; Sorrell et al. 2000), allowing *T. domingensis* to maintain rapid nutrient uptake and relatively high photosynthetic rates in flooded soil (Koch et al. 1990; Pezeshki et al. 1996). The O_2-transport mechanisms of *Typha* can also have secondary effects on methane (CH_4) emissions from wetlands (*see Carbon and greenhouse gas*) (Chanton et al. 1993; Chanton and Whiting 1996; Rose and Crumpton 1996; Faußer et al. 2012).

Sexual Reproduction through Seeds

Typha plants are monoecious, with both male and female flowers in an inflorescence (flower cluster); inflorescences develop as spikes at the tips of erect stems. Each inflorescence spike is two-tiered, with yellow, male, staminate flowers on the narrow top and brown, female, pistillate flowers on the broader portion below (Smith 2000) (Fig. 1). The gap between male and female inflorescence regions can generally be used to distinguish species, although distinguishing *T.* × *glauca* is less reliable based on morphology. *Typha latifolia* male and female inflorescences touch, whereas there is usually a gap between inflorescences for *T. angustifolia* (5–120 mm), *T.* × *glauca* (0–33 mm), and *T. domingensis* (0–8 mm) (Finlayson et al. 1985; Grace and Harrison 1986). Male flowers release up to 420-million pollen grains per inflorescence in spring, while female flowers release the single-seeded fruits in late summer (Mitich 2000). The small (<100 μg), wind-dispersed fruits can number 20,000–700,000 per inflorescence and travel more than 1 km to colonize distant wetlands (Yeo 1964; Stewart et al. 1997; Mitich 2000; Baldwin and Cannon 2007). Elongated hairs on the stalk supporting the fruit aid in wind dispersal; if the fruits land in water, the hairs close, the fruit wall splits, and the single seed is released and sinks (Grace and Harrison 1986; Smith 2000). Seeds can germinate rapidly (within 2–20 days), but ungerminated seeds can remain viable in the soil and form a persistent seed bank (Leck and Simpson 1987; Stewart et al. 1997; Lorenzen et al. 2000).

Typha seeds have a number of environmental requirements for successful germination: moisture, temperature, light, and O_2 all influence germination (Sifton 1959; Bedish 1964; Bonnewell et al. 1983; Welling et al. 1988; Ekstam and Forseby 1999; Ahee et al. 2015). Under field conditions, most germination occurs on exposed, saturated soils (Weller 1975; Beule 1979; Lorenzen et al. 2000), although seeds can germinate under water (Bedish 1964). Light is required for germination (Grace and Harrison 1986; Lorenzen et al. 2000), which limits germination in clear water deeper than 40 cm (Sifton 1959; Beule 1979) or in sediment deeper than 1 cm (Galinato and van der Valk 1986). Cold stratification is not an obligate requirement for *T.* × *glauca* (Galinato and van der Valk 1986), whereas other species (*T. latifolia*, *T. domingensis*) show greatest germination at higher temperatures (>30 °C) (Bonnewell et al. 1983; Lorenzen et al. 2000).

When the seeds germinate and seedlings begin to grow, they may be submerged in shallow (2.5 cm) water or on saturated soil (Bedish 1964; Beule 1979). They produce a series of small juvenile leaves then begin to produce the erect leaves typical of adult plants (Mitich 2000, for *T. latifolia*). Because the seeds are small compared to those of many co-occurring species (Leck and Simpson 1993), seedlings do not have abundant seed resources to draw on and must establish and grow quickly. Flooding soon after germination caused mortality in *Typha* seedlings, but after a month, seedlings could grow in water up to 40 cm deep (Beule 1979). Seedling success depends on appropriate light, temperature, and hydrology but also on water and substrate chemistry, including nutrient and auto-inhibitor (allelochemicals produced by *Typha* species) levels (McNaughton 1968; Grace and Harrison 1986; Gallardo et al. 1998; Smith and Newman 2001; Jarchow and Cook 2009). Seedling establishment appears to be rare, relying on gaps or other disturbances that create appropriate light environments (Leck and Simpson 1993).

Asexual Reproduction through Rhizomes

After seedling establishment, *Typha* develops axillary rhizomes with roots that anchor plants into wetland sediments (Fig. 2c). Rhizome tips turn erect to produce upright ramets (i.e., culms) with elongated linear leaves that form dense, nearly monospecific stands in wetlands; these stands can cover an area of 40–80 m^2 within months to years (Yeo 1964; Grace and Harrison 1986). Field sampling in the Great Lakes region demonstrated that rhizomes can grow horizontally at least 76 cm in a summer in 60–75 cm deep water (D. Albert personal observations November 2018). Rhizomes also store energy-rich carbohydrates and nutrient reserves during the winter; these reserves are mobilized in spring to support rapid growth of new shoots (i.e., ramets) (Kausch et al. 1981; Hogg and Wein 1987; Garver et al. 1988; Steinbachová-Vojtíšková et al. 2006; Asaeda et al. 2008; Tursun et al. 2011). *Typha* can also survive as floating mats that can then colonize newly disturbed sites.

Habitat

Hydrology

According to the National Wetland Plants List of the US, species of *Typha* are considered obligate wetland plants, meaning they cannot survive in non-wetland habitats (Lichvar et al. 2016). As such, *Typha* is found in a wide variety of wetland habitats including marshes, shores, streambanks, ditches, and margins of lakes and ponds, and tidal wetlands showing a tolerance for a range of water levels (Harris and Marshall 1963; Stewart and Kantrud 1972; Newman et al. 1998; Safratowich et al. 2008).

Typha invasions into natural wetlands are often associated with hydrologic alterations. *Typha* is flood-tolerant and generally favored by moderate flooding (Harris and Marshall 1963; Bedish 1967; Grace and Wetzel 1982a; Grace and Harrison 1986; van der Valk 1994; Kercher and Zedler 2004; Li et al. 2004; Boers et al. 2007; Asamoah and Bork 2010). Periodic high water levels and prolonged flooding to depths >1 m may reduce or eliminate populations (McDonald 1955; Harris and Marshall 1963; Farney and Bookhout 1982; Grace and Wetzel 1982a; de Swart et al. 1994; van der Valk 1994; Kowalski and Wilcox 1999), and periodic low water levels with resultant low soil moisture can also hinder *Typha* (Urban et al. 1993; Wilcox et al. 2008). *Typha* has some tolerance to drought and can colonize wetlands under drought conditions (Swanson et al. 2003) provided soils have relatively low redox potential from sufficient periods of anoxia (Pezeshki et al. 1996). Hydrologic (e.g., water depth) variability tends to keep *Typha* under control (Boers and Zedler 2008). Lack of variability (e.g., due to water-level control) can reduce extremes and provide elevation zones where *Typha* is never stressed and can therefore form near-monotypic stands (Shay et al. 1999; Wilcox et al. 2008). In addition, *Typha* invasion can be enhanced by hydrologic alterations that raise the water table and create wetter soil conditions (see *Regional problems*). *Typha latifolia* is often favored in shallower waters, while *T. angustifolia*, *T.* × *glauca*, and *T. domingensis* are better adapted to deeper waters (Grace and Harrison 1986; Grace 1988, 1989; Waters and Shay 1990, 1992; Weiner 1993), though it is not uncommon for multiple species of *Typha* to be found occupying the same wetland zones (Grace and Wetzel 1982b; McKenzie-Gopsill et al. 2012; Pieper et al. 2018).

Chemistry

Sediment and water chemistry strongly influence *Typha* growth and survival. *Typha* is often outcompeted by other aquatic macrophytes in low-nutrient, oligotrophic conditions (Newman et al. 1996; Currie et al. 2014). Increased nitrogen (N) and phosphorus (P) concentrations in wetland waters due to fertilizer runoff from agricultural fields promote the growth of *Typha*, allowing it to proliferate aggressively in nutrient-enriched freshwater wetlands and brackish salt marshes (Boyd and Hess 1970; Newman et al. 1996; Miao and Sklar 1998; Galatowitsch et al. 1999) (*see Nutrients*).

Typha's salt tolerance is generally lower than many halophytic aquatic macrophytes. *Typha* can be found in fresh, moderately brackish, and brackish but not highly saline waters (Stewart and Kantrud 1972; Beare and Zedler 1987; Zedler et al. 1990; Glenn et al. 1995). *Typha's* salt intolerance restricts it from occurring in the most saline marine environments (>30 ppt) (Crain et al. 2004) and inland saline wetlands (Swanson 1992). *Typha angustifolia* can tolerate more saline conditions than *T. latifolia*, while *T.* × *glauca's* salinity tolerance falls in between the two parental species (Stewart and Kantrud 1972; Wilcox 1986; Grace and Harrison 1986). *Typha domingensis* is three-times more tolerant of sulfide than *Cladium* in the Everglades (Li et al. 2009). *Typha* also can grow in soils contaminated with heavy metals (e.g., Al, As, Cd, Cr, Cu, Hg, Mn, Ni, Pb, and Zn) (Manios et al. 2003; Jacob and Otte 2004; Tang et al. 2005; Bonanno and Cirelli 2017) and has been used to remediate contaminated water and soils in natural and constructed wetlands (*see Bioremediation*)

(Allen and Kleinmann 1991; Mbuligwe 2004; Cicek et al. 2006).

Genetics

Hybridization between native and non-native species or genotypes is one of the primary drivers behind the evolution of invasiveness (Arnold 1997; Ellstrand and Schierenbeck 2000), often closely following species introductions (Abbott 1992; Rhymer and Simberloff 1996). For *T.* × *glauca*, in the majority of cases, *T. angustifolia* is the maternal parent and *T. latifolia* is the paternal parent (Ball and Freeland 2013; Freeland et al. 2013). Recent research using chloroplast DNA (cpDNA) suggests that *T.* × *glauca* may be a three-way hybrid involving *T. latifolia*, *T. angustifolia*, and an introgressed cpDNA lineage from an unidentified *Typha* genotype (Freeland et al. 2017). Pollen morphology has been used to identify *T. latifolia*, *T. angustifolia*, and their hybrids (Finkelstein 2003; Lishawa et al. 2013; Marburger 2013).

Typha species and hybrids are most conclusively identified using nuclear DNA microsatellite markers and cpDNA, which is possible because some of these DNA markers are associated only with one or the other parental species (Tsyusko-Omeltchenko et al. 2003; Snow et al. 2010; Kirk et al. 2011; Freeland et al. 2017). Six species-diagnostic microsatellite loci were used in studies in seven US Great Lakes national parks (Travis et al. 2010; Marburger and Travis 2013). The results of genetic analysis of adult and seed bank *Typha* populations revealed that F1 hybrids (i.e., the first-generation offspring of pure *Typha* species, Fig. 3) can account for up to 99% of individuals. Other genetic studies have repeatedly found F1 hybrids throughout the northeastern and midwest regions of the US (Kirk et al. 2011; Freeland et al. 2013), as well as in California and possibly Florida (S. Travis, unpublished data; note that *T. domingensis* microsatellite alleles have yet to be characterized, with preliminary evidence suggesting size overlap with those of *T. angustifolia*).

Seed production can be affected by parental genotypes. When *T.* × *glauca* is pollinated by either parental species (referred to as ‘backcrossing’; Fig. 3), seed production by *T.* × *glauca* offspring was relatively high. When *T.* × *glauca* was pollinated by other *T.* × *glauca* (referred to as ‘advanced-generation’ or ‘F2’ hybrids), its seed production was 75% lower, indicating reduced hybrid fertility (Pieper et al. 2017). However, even with relatively low hybrid fertility, there are viable seeds that allow *T.* × *glauca* to proliferate and spread independent of its parental species.

Competition and Hybrid Vigor

In the parts of North America where *T. angustifolia*, *T. latifolia*, and *T.* × *glauca* overlap, *T.* × *glauca* dominates wetlands at the expense of both parental species (Travis et al. 2010; Kirk et al. 2011; Freeland et al. 2013), where it typically achieves much larger clone sizes (Travis et al. 2011), given that all three taxa can occupy similar habitat types (Olson et al. 2009; McKenzie-Gopsill et al. 2012; Zapfe and Freeland 2015; Pieper et al. 2018). The success of invasive hybrids can often be explained by heterosis, or hybrid vigor, which arises when hybrids have better fitness than parental species; there is some evidence for this in *T.* × *glauca.* For example, at one site in Ontario, Canada, *T. latifolia* was the tallest plant at the beginning of the growing season, but F1 hybrids quickly attained and maintained a greater height than either parental species (Zapfe and Freeland 2015). Similarly, common garden experiments found that hybrids outperformed *T. latifolia* in terms of total and aboveground biomass (Bunbury-Blanchette et al. 2015). Hybrids may also limit the fecundity of *T. latifolia* because hybrid pollination of *T. latifolia* stigmas by *T.* × *glauca* does not result in viable seeds (Pieper et al. 2017). Finally, *T.* × *glauca* produces copious leaf litter, which negatively affects the growth of competing plants (Vaccaro et al. 2009; Larkin et al. 2012a). Leachate from *T.* × *glauca* leaf litter also inhibits the germination of *T. latifolia* and *T. angustifolia* seeds while having no effect on *T.* × *glauca* seed germination (Szabo et al. 2018).

Section 2: Regional Problems with *Typha* Invasion in North America

The taxa of *Typha* in North America have expanded their range and abundance over the last 50–100 years, particularly in regions such as the Laurentian Great Lakes (LGL), Florida Everglades, and midwestern Prairie Pothole Region (PPR; Fig. 4). Here, we present case studies from each of these three

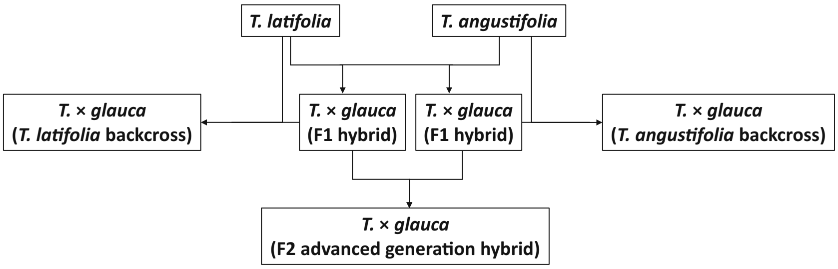

Fig. 3 Pathways of hybrid *T.* × *glauca* formation between *T. latifolia* and *T. angustifolia*

regions. The specific circumstances and timelines for expansion are unique to each region, albeit there are also common mechanistic drivers among regions. In particular, increased nutrient inputs into wetlands from agricultural runoff and disruption of natural hydrologic regimes are repeatedly identified as underlying drivers of *Typha* invasion. Corridors associated with roads and railroads, as well as boat travel, are also likely drivers of *Typha* expansion.

Laurentian Great Lakes and Manitoba Coastal Wetlands

Historical Presence and Current Extent

The Laurentian Great Lakes (LGL) region has thousands of kilometers of coastal lacustrine wetlands in the US and Canada that host a number of invasive plants, including *Typha* species. Three taxa of *Typha* occur in LGL wetlands: *T. latifolia*, *T. angustifolia*, and *T.* × *glauca.* While pollen records indicate that *T. latifolia* is native to eastern North America, pollen and herbarium records show increased abundance of *T. latifolia,* as well as westward invasion and proliferation by *T. angustifolia*, into LGL coastal wetlands beginning in the mid-1800s (Galatowitsch et al. 1999; Shih and Finkelstein 2008). The first known herbarium collection of *T. angustifolia* was from a Lake Ontario marsh in Oswego, New York, in 1880 (Wibbe 1880), followed by a Lake Erie coastal marsh in 1882 (Miller 1882), and a southern Lake Michigan coastal wetland in 1895 (Umbach 1895). *Typha* × *glauca* is largely missing from early herbarium records, most likely because hybridization was not widely recognized. However, *T.* × *glauca* occurred in LGL coastal wetlands at least since 1909, when its presence was documented at Illinois Beach on southern Lake Michigan (Gates 1912). Data from the Great Lakes Coastal Wetlands Monitoring Program illustrate the current extent of invasive *Typha* (*T.* × *glauca* and *T. angustifolia*) in the LGL. Between 2011 and 2013, invasive *Typha* were the dominant plant taxa in 13.5% of all LGL coastal wetland areas (Carson et al. 2018), where dominance is defined as ≥25% cover (Frieswyk et al. 2007). Lake Ontario has the highest level of invasive *Typha* dominance, at nearly 50% of wetland area, followed by Lake Erie (22%), Lake Michigan (12%), Lake Huron (6%), and Lake Superior (1%).

Similar to the LGL system, the large lakes in Manitoba Canada have also undergone widespread *Typha* invasion. Shay et al. (1999) used aerial photographs to map changes in vegetation types at specific sites in Delta Marsh of Lake Manitoba from 1948 to 1997. They indicate invasion of the hybrid *T.* × *glauca* first occurred in Delta Marsh during a period following extensive flooding during the 1950s. Using historical aerial photography Grosshans (2001) constructed vegetation maps of the entire Delta Marsh and examined long-term changes in vegetation communities over a 36-years period (1965–1997), documenting the considerable invasion of *Typha* throughout this coastal wetland system.

Ecological Drivers of *Typha* Invasion

Laurentian Great Lakes coastal wetlands are naturally dynamic ecosystems due primarily to variability in water levels over a range of time scales. Over decades, lake water levels vary by as much as 2 m (Gronewold et al. 2013), shifting the shallow-sloping shorelines by up to several hundred meters and resulting in broad changes in soil inundation, wetland conditions, and vegetation zonation (Minc 1997; Albert et al. 2005). Laurentian Great Lakes wetlands typically consist of three water-level-mediated herbaceous vegetation zones: wet meadow, emergent marsh, and submergent marsh. Periodic water-level changes maintain plant diversity by disturbing successional trajectories and shifting the breadth, extent, and location of vegetation zones (Wilcox 2004). Following water-level retreat, wind-dispersed seeds and those in seed banks germinate on exposed mudflats (Keddy and Reznicek 1986), and long-

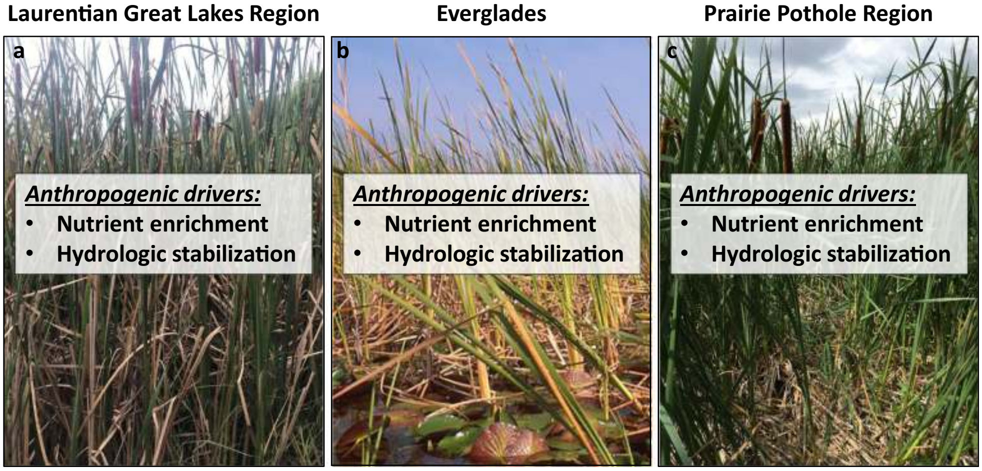

Fig. 4 *Typha* invasion has been particularly aggressive in North America in part due to nutrient enrichment from agricultural runoff and hydrologic stabilization: **a** the Laurentian Great Lakes Region, **b** the Florida Everglades, and **c** the midwestern Prairie Pothole Region

term persistent rhizomatous species emerge. In less perturbed LGL wetlands, *T. latifolia* typically persists as a subdominant plant-community member, occurring primarily at the margin between the emergent marsh and wet meadow communities. However, anthropogenic disturbances to natural nutrient and hydrologic regimes tend to favor invasive *Typha* over native plants in LGL wetlands.

Studies from around the LGL region have demonstrated that anthropogenic hydrologic disturbances enhance the competitive ability of *Typha*. *Typha* tolerates a wide range of water levels (Waters and Shay 1990; Bunbury-Blanchette et al. 2015), exhibiting increased competitive dominance under continuously-flooded conditions (Boers and Zedler 2008), prolonged low water levels (Lishawa et al. 2010), and when exposed to rapidly changing water levels (Hall and Zedler 2010). Reduced hydrologic variability and stabilized, above-average water levels, resulting from water-level control on Lake Ontario, have resulted in increased dominance by invasive *Typha* and the widespread displacement of wet-meadow communities (Wilcox and Meeker 1995; Wilcox et al. 2008). In-depth studies of large-scale *Typha* invasion took place on Lake Ontario, which became a regulated reservoir beginning around 1960 following construction of the St. Lawrence Seaway (Wilcox and Meeker 1995; Hudon et al. 2006; Wilcox and Xie 2007; Wilcox et al. 2008; Wilcox and Xie 2008). The annual variability was reduced from 1.5 to 0.7 m, and low lake levels during the growing season no longer occurred, even in years with low water supply. Detailed analyses of aerial photographs spanning a period from the 1950s–2001 showed that upslope wet meadows were continuously being lost to invasion by *Typha* (Wilcox et al. 2008). The results indicated that *Typha* invaded lakeward by forming floating mats, while landward invasion was more pervasive and occurred at the expense of grasses and sedges since sustained higher lake levels allowed *Typha* to outcompete sedges and grasses more tolerant of drier soil conditions. These findings corroborate those of Wilcox et al. (1984) in which vegetation types in the Cowles Bog Wetland Complex at Indiana Dunes National Lakeshore (adjacent to southern Lake Michigan) were mapped using aerial photographs from 1938 to 1982. They concluded that *Typha* invasion of sedge-grass meadow was promoted by continually wet conditions that resulted from seepage from a diked pond on adjacent lands. Stabilized high water levels have also been linked to increased dominance and faster rates of *T.* × *glauca* spread in interior Illinois (Boers et al. 2007) and Wisconsin wetlands, where *T.* × *glauca* clones can spread at rates of up to 4 m in diameter per year (Boers and Zedler 2008). Competitive dominants, such as *Carex* spp. (sedges), expand more slowly via vegetative growth and have reduced seedling survival under flooded conditions (Hall and Zedler 2010).

Similarly, in the Manitoba lakes, regulation of lake levels induced an expansion of *Typha* upgradient into *Phragmites australis* (common reed) communities and downgradient into open, shallow water. Extensive studies at Delta Marsh showed that *Typha* expanded in response to increasing and stable water levels (Waters and Shay 1990, 1992; Shay et al. 1999; Seabloom et al. 2001) and did so by vegetative growth from small colonies found in openings created by past extreme flooding (de Swart et al. 1994; Seabloom et al. 2001). At neighboring Lake Winnipeg, Grosshans et al. (2004) concluded that *Typha* invasion was partly related to lack of periodic low water levels following regulation of lake levels. Additionally, water-level control resulted in loss of emergent vegetation and erosion of uplands separating adjoining water bodies resulted in the amalgamation and expansion of marsh bays (Grosshans et al. 2004).

Plant communities tend to be more susceptible to invasions when disturbance to vegetation co-occurs with eutrophication (Burke and Grime 1996). This pattern holds in LGL and Manitoba coastal wetlands, where *Typha* tends to become dominant in hydrologically-disturbed and nutrient-enriched sites, such as within dikes (Thiet 2002; Herrick and Wolf 2005), where wetlands have been isolated from natural hydrologic variability and nutrient exchange with lakes (Mitsch 1992; Hill et al. 1998). Herrick and Wolf (2005) found that diked LGL wetlands had greater soil organic matter, plant available nutrients (N, P, potassium [K]), and more than double the *Typha* cover than in paired, undiked wetlands (58.5% vs. 21.7%). Sustained flooding benefits *Typha* in part because under anoxic conditions, P becomes more biologically available (Young and Ross 2001), and *Typha* is able to use excess N and P more efficiently than native sedge and rush species that they displace (Woo and Zedler 2002; Larkin et al. 2012b). As such, *Typha* exhibits greater P retention and growth when persistently inundated (Boers and Zedler 2008). Prolonged low-water conditions have also been linked with increased presence and dominance of invasive *Typha* (Tulbure et al. 2007). These low-water effects have been documented even in otherwise-intact northern LGL coastal wetlands (Lishawa et al. 2010), likely due to increasing propagule pressure in the region. However, *T. angustifolia* stands were less robust after several low-water years, leading to lower stem density and invasion by herbaceous meadow and wetland tree species (Albert and Brown 2008). Extensive stands of *T. angustifolia* were also replaced by invasive *P. australis* in the southern LGL during the low-water period that began in 1999 (Albert and Brown 2008).

Florida Everglades

Historical Presence and Current Extent

The Everglades is a large, oligotrophic, subtropical wetland, covering approximately 7900 km^2 in southern Florida (Light and Dineen 1994). It consists of a mosaic of plant communities that occur along topographic gradients from deepwater sloughs, to wet prairies, to *Cladium*-dominated communities, to marl prairies and tree islands (Davis and Ogden 1994; Gunderson 1994). *Typha domingensis* and *T. latifolia* are considered native in this landscape. While there are some references to *T. angustifolia*, multiple databases listing Typhaceae do not include Florida as within the range of *T. angustifolia* (Flora of North America 2000; Gann et al. 2001–2018; Wunderlin et al. 2018). As noted elsewhere, while artificial hybridization and putative field hybrids of *T. domingensis* and *T. latifolia* have been reported in California (Smith 1967), natural hybrids are found in few locations and are reportedly highly sterile (Flora of North America 2000). To date, there is no clear evidence of hybridization of these species in the Everglades, and in general, even intraspecific genetic variation within *Typha* populations is very low (Zhang et al. 2008).

Much of the documentation of *Typha* within the Everglades has focused on the northern and central parts of the ecosystem, where *Typha* is abundant on the periphery of the system (i.e., adjacent to canals; Fig. 5), especially in close proximity to inflow structures, but is generally sparse within the interior marsh (Rutchey et al. 2005; Rutchey et al. 2008; Gann and Richards 2014). For example, *Typha* relative abundance estimated using 400-m grids in Water Conservation Areas (WCAs) 1 and 2A, the two northernmost impoundments (Fig. 5), was 13% (Gann and Richards 2014). More recently, *Typha* invasions have been documented in the southern Taylor Slough within Everglades National Park (Surratt et al. 2012). In 2014, vegetation mapping within 63, 1-km^2 sites throughout the Everglades landscape documented that *Typha* alone or *Typha* with *C. jamaicense* or shrubs occurred in 60% of the sites with cover ranging from <1%, 1–5%, and 5–26% in 37, 45, and 18% of the sites, respectively. While systemwide mapping of *Typha* has not been conducted for over a decade, there is evidence that in some areas the rate of expansion is declining in response to reductions in P loading to the Everglades (Rutchey et al. 2008; Zweig and Newman 2015). For example, in WCA-2A, the average annual rate of *Typha* expansion decreased from 961 ha y^{-1} during 1991–1995, to 312 ha y^{-1} during 1995–2003 (Rutchey et al. 2008).

Ecological Drivers of *Typha* Invasion

Everglades plant communities developed within a sub-tropical, rain-driven, flat carbonate system. As a result, most populations within the pristine Everglades are adapted to periodic fire, fluctuating hydroperiod, and low nutrient (specifically P) conditions (Davis 1943; Steward and Ornes 1983; Gunderson 1994; Richardson et al. 2008a). Low nutrient availability is not conducive to *Typha* species dominance, thus *Typha* in the undisturbed Everglades historically occurred as scattered diffuse stands (Davis 1994), with small pockets associated with nutrient-enriched areas such as wading-bird colonies or alligator holes. However, starting in the 1800s, canals were dug within the northern Everglades to drain the peatlands for agriculture and provide flood control for urban development along the northern and eastern portions (Light and Dineen 1994). The remnant Everglades system is composed of impoundments, WCAs and Everglades National Park. Today, instead of the historical, rain-driven sheet flow, water moves through the ecosystem via approximately 3380 km of canals, >1200 culverts and water control structures, and 77 pump stations (South Florida Water Management District 2018). This altered hydrology has had a significant impact on the vegetation. *Typha* expanded into large areas of the Everglades primarily as a result of P enrichment from agricultural runoff (Urban et al. 1993; Davis 1994; Newman et al. 1996; Craft and Richardson 1997; Miao and Sklar 1998; Miao and DeBusk 1999; McCormick et al. 2002; Childers et al. 2003; Sklar et al. 2005; Noe and Childers 2007; Richardson 2008; McCormick et al. 2009). *Typha* has been able to outcompete other species due to its rapid growth rate and high plasticity that can take advantage of P enrichment (Lorenzen et al. 2001; Vymazal and Richardson 2003). By contrast, *C. jamaicense*, the dominant species of the Everglades ridge community, is adapted to low P conditions; *C. jamaicense* has high production of acid phosphatase extracellular enzymes for P acquisition under low P conditions (Lorenzen et al. 2001; Kuhn et al. 2002; Webb and Zhang 2013). The shape and arrangement of *Typha* invasion in a nutrient-enriched portion of the northern Everglades tends to follow the pattern of historic sloughs (Fig. 5) (Rutchey and Vilchek 1999), suggesting that sloughs may be particularly susceptible because of the deeper water and low stature, predominantly floating-leaved vegetation (McCormick et al. 2009). In addition, upon nutrient enrichment in sloughs, the native floating periphyton disappears, and remnant communities have low biomass due to shading created by tall, dense *Typha* stands (McCormick et al. 1997; Vaithiyanathan and Richardson 1999; Gaiser et al. 2005; Gaiser et al. 2011; Hagerthey et al. 2011).

Disturbances, such as changes in hydrology, overdrainage, or fire, also provide a competitive advantage to *T. domingensis* in the peat-based Everglades system (Gunderson 1994; Newman et al. 1998; Miao et al. 2001; Smith and Newman 2001; Smith et al. 2001; Richardson 2008; Tian et al. 2010; Wu et al. 2012). Increased water depth (Newman et al. 1996) and flooding duration (Urban et al. 1993) allow *T. domingensis* to outcompete *C. jamaicense. Typha* aboveground tissues conduct pressurized bulk air flow during the day (Chanton et al. 1993) that oxygenates its rhizosphere (Chabbi et al. 2000) and enables it to withstand the reduced conditions caused by flooding. In drained conditions, however, *T. domingensis* expansion results from soil oxidation, which can result in P release (Newman et al. 1998).

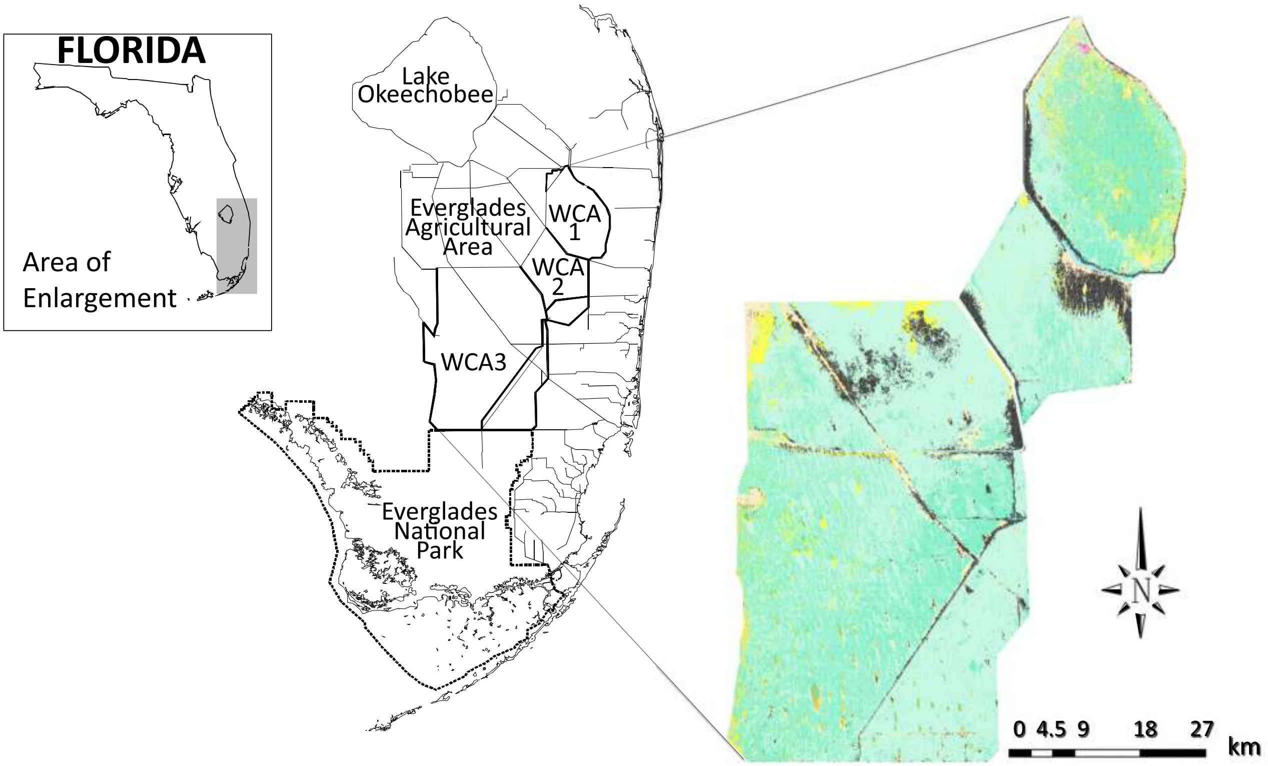

Fig. 5 The spatial extent of *Typha* (black shading) throughout the northern and central Everglades observed in 2003–2004 (Rutchey et al. 2008; Sklar et al. 2009, 2011). Note the extensive *Typha* coverage adjacent to canal systems

Similarly, both peat burns and surface vegetation burns promote *T. domingensis* expansion through the release of bioavailable P (peat burn only) and the creation of openings that alleviate competition and create opportunities for invasion (Smith and Newman 2001; Richardson et al. 2008a; Richardson et al. 2008b). *Typha domingensis* invasion has historically occurred in the north-central Everglades (i.e., WCAs, Fig. 5). Detailed north-to-south transects in WCA-2A from 1990 until 2002 showed that *T. domingensis* densities were dominant in the more eutrophic sites close to canal P loadings, while *C. jamaicense* dominated less-impacted or oligotrophic sites further in the interior away from the canals (Miao and Sklar 1998; Richardson 2008).

Once established, *Typha* dominance can be maintained for prolonged periods, even when nutrient loads to the system are reduced. With roots predominantly within the upper 20 cm (Miao and Sklar 1998) but extending deeper, *Typha* is able to 'mine' legacy P in nutrient-enriched soils, translocating P from soils back into the water column; such mining presents a long-term source of P even after reductions in P loading into the Everglades (Noe and Childers 2007; Richardson et al. 2008b). In addition, the rapid growth of *Typha* in nutrient-enriched areas results in the rapid accumulation of peat (0.5–>1 cm y^{-1} compared to ~1 mm yr.$^{-1}$ in unenriched areas (Reddy et al. 1993; Craft and Richardson 1997). This in turn creates higher elevations that are more susceptible to drying and more favorable to transitional wetland species such as *Salix caroliniana* (coastal plain willow).

The Prairie Pothole Region

Historical Presence and Current Extent

The Prairie Pothole Region (PPR) contains millions of shallow, depressional wetlands, commonly referred to as 'potholes,' which are nested within a cropland and grassland matrix (Euliss et al. 2006; Badiou et al. 2011; Dahl 2014). Potholes generally are classified as palustrine emergent wetlands with periods of inundation ranging from ephemeral to permanent (Stewart and Kantrud 1971; Cowardin et al. 1979), mean water depths ranging from less than 0.5–2 m (Stewart and Kantrud 1972; Dahl 2014; Tangen et al. 2015), and salinities ranging from fresh to hypersaline (Stewart and Kantrud 1972; Swanson et al. 1988; LaBaugh 1989; Euliss et al. 2014; Goldhaber et al. 2014; Mushet et al. 2015a).

According to historical accounts and reviews, *Typha* was not prominent in the PPR prior to the mid-twentieth century (Kantrud 1986, 1992; Sojda and Solberg 1993; Galatowitsch et al. 1999). In the North Dakota State University (NDSU) Herbarium, the earliest collection of *T. latifolia* in North Dakota was in 1891, and seven additional collections were made from 1906 to 1912 (Dekeyser, NDSU Herbarium Curator, pers. obs). The first collection of *T. angustifolia* was in 1942, and the first verified specimen of *T.* × *glauca* was in 1963. Since that time, *Typha* has become ubiquitous throughout the region (Stewart and Kantrud 1972; Kantrud 1986; Ralston et al. 2007; Safratowich et al. 2008; Post van der Burg et al. 2014). Potholes have been associated with *T. angustifolia* and *T. latifolia*, and *T.* × *glauca* has become dominant in many areas (Stewart and Kantrud 1971, 1972; Kantrud 1986). In the North Dakota portion of the PPR, Ralston et al. (2007) showed that 23–49% of wetlands surveyed contained *Typha* depending on location in the PPR. Also, Ralston et al. (2007) suggested that wetlands with *Typha* were, on average, larger than the wetlands without *Typha* and that *Typha* covered 37% of individual wetlands.

Ecological Drivers of *Typha* Invasion

In their natural state, PPR wetlands are characterized by dynamic vegetation zones, which are composed of distinct plant communities that fluctuate seasonally, as well as with wet and dry annual cycles (Euliss et al. 2004; van der Valk 2005; Euliss and Mushet 2011). These dynamic shifts between inundated and dry conditions generally do not favor establishment and persistence of dominant, monotypic vegetation communities. Historic grazing and wildfire regimes of prairie ecosystems also precluded establishment of such vegetation communities.

Natural disturbances, such as grazing and fire that preclude *Typha*, are no longer prominent in many areas, while anthropogenic disturbances such as tillage, siltation, and drainage result in environments where *Typha* flourishes (Kantrud 1986; Swanson and Duebbert 1989; Gleason and Euliss 1998; Anteau 2012; Wiltermuth and Anteau 2016). Many potholes exist within agricultural fields where they can receive nutrient and sediment inputs that promote the spread of *Typha* (Martin and Hartman 1987; Wang et al. 1994; Kantrud and Newton 1996; Gleason and Euliss 1998; Werner and Zedler 2002; Woo and Zedler 2002; Tangen et al. 2015). Sedimentation can inhibit seed germination of other species and reduce water depths of potholes (sediment filling) so that they no longer exceed depths that are detrimental to *Typha* (Jurik et al. 1994; Wang et al. 1994; Gleason and Euliss 1998). Soil structure and hydrology of a wetland can be considerably modified by sedimentation via a decrease in soil organic matter and an increase in soil bulk density (Werner and Zedler 2002), which favor *Typha* over native species. Wetlands in a cropland matrix also can receive greater inputs of precipitation runoff, resulting in lengthened periods of the saturated or moist-soil conditions preferred by *Typha* (Euliss and Mushet 1996; van der Kamp et al. 2003). Lastly, while salinity of potholes varies greatly across spatial and temporal scales, the majority of wetlands fall within ranges that support *Typha* (Stewart and Kantrud 1971, 1972; Ralston et al. 2007; Gleason et al. 2009); and recent wetting of potholes in response to increased precipitation inputs (Mushet et al. 2015b) has likely increased the number capable of supporting *Typha*.

Wetlands of the PPR landscape exist in intermittently-connected watersheds characterized by smaller, more ephemeral wetlands in the upper parts of the watershed and larger, more permanent wetlands in the lower parts of the watershed (McCauley and Anteau 2014; Hayashi et al. 2016). Demand to increase agricultural production has motivated the drainage of many PPR wetlands, which has been particularly focused on the drainage of smaller, more ephemeral wetlands (Dahl 1990) into larger wetlands through either surface ditches or subsurface drainage systems (i.e., ‘consolidation drainage’) (Krapu et al. 2004; Anteau 2012; McCauley et al. 2015). Wetlands that receive drainage water have markedly greater and more stable water levels than they did before drainage (Wiltermuth 2014; McCauley et al. 2015; Anteau et al. 2016). Additionally, the PPR has experienced record-high water levels since the mid-1990s due to changes in climate and weather patterns, increasing the amount of water entering wetlands even in areas that do not have a large degree of consolidation drainage (Anteau et al. 2016; McKenna et al. 2017). These effects of land use and climate have a synergistic interaction that increases water levels of basins until they stabilize at their basin spill point (McCauley et al. 2015; Anteau et al. 2016; Post van der Burg et al. 2016). While increases in water level can reduce *Typha* abundance in the short term, the eventual stabilized conditions can promote proliferation of *Typha* over time (Shay et al. 1999; Euliss et al. 2004; Anteau 2012; Wiltermuth and Anteau 2016).

Section 3: Ecological, Biogeochemical and Agricultural Impacts of *Typha* Invasion

The invasion and subsequent dominance of wetlands by invasive *Typha* result in predictable patterns of change at nearly all trophic levels in wetland ecosystems (Angeloni et al. 2006; Mitchell et al. 2011; Lishawa et al. 2013; Lishawa et al. 2014; Lishawa et al. 2017) (Fig. 6).

Fig. 6 *Typha* invasion impacts nearly all trophic levels in and around wetland ecosystems: **a** native vegetation - standing dead *Typha* from previous years' growth forms dense cover that inhibits competing plant establishment; **b** waterbird breeding habitat - Canvasback (*Aythya valisineria*) nesting in *Typha*; **c** muskrat den building material; **d** deer cover; **e** northern pike spawning habitat; **f** invertebrate habitat; **g** amphibian habitat; **h** pollinator habitat; **i** agriculture - sunflower damage from blackbirds that roost in *Typha* stands

Flora and Fauna

Plants

Invasive *Typha* dominance impacts the diversity and abundance of a range of native taxa, decreasing plant diversity (Frieswyk and Zedler 2007; Wilcox et al. 2008; Farrer and Goldberg 2009; Tuchman et al. 2009), altering plant-community structure (Grosshans et al. 2004; Lishawa et al. 2010), and modifying the physical structure of vegetation (Lishawa et al. 2017). Both direct and indirect mechanisms are responsible for the displacement of native plant species by invasive *Typha*. Directly, *Typha* has higher rates of primary productivity (Tuchman et al. 2009) and more efficient use of excess nutrients (Woo and Zedler 2002; Larkin et al. 2012b), conferring competitive dominance over native sedges. Indirectly, standing-dead leaf litter in *Typha* stands accumulates to the detriment of native species, while minimally affecting *Typha* growth rates (Farrer and Goldberg 2009; Tuchman et al. 2009; Vaccaro et al. 2009; Mitchell et al. 2011; Larkin et al. 2012a) (Fig. 6a)., except when litter was experimentally applied to a depth of 50 cm, which caused a decreased in *Typha* productivity (Jordan et al. 1990).

Data collected from stand-age gradients in the field and from long-term mesocosm experiments indicate that, with increasing stand-age, litter mass and cover, *Typha* density, soil organic matter, organic sediment depth, and soil denitrification potential tend to increase, while plant species richness and evenness decrease (Mitchell et al. 2011; Lishawa et al. 2014). Thus, time since a site has been invaded serves as a useful proxy for degradation of the system and its potential for restoration.

Waterfowl and Wildlife

Dense stands of *Typha* eliminate open-water zones and replace other emergent species and submerged aquatic species (Kantrud 1992; Cressey 2016; Lawrence et al. 2016a). *Typha* impacts wildlife principally by displacing forage-producing plants and altering vegetative structure that many wildlife species are dependent upon (Kantrud 1986).

Prior to the invasion of *Typha*, communities of emergent annual and perennial plants that occupy less permanently ponded parts of wetlands typically have greater diversity (e.g., *Polygonum* [knotweed], *Carex, Eleocharis* [spikerush], *Scirpus* spp. [bulrush], *Schoenoplectus* [bulrush]) (Kantrud 1986; Weller 1988; Cressey 2016). These emergent plants produce great densities of seeds that are consumed by many waterbird species (Krapu and Reinecke 1992; Haukos and Smith 1993; Dugger et al. 2007; Greer et al. 2007; Hagy and Kaminski 2012). In contrast, *Typha* seeds are very small and not considered a wildlife food. *Typha* also expands into more permanently ponded parts of wetlands that typically have submerged, aquatic-vegetation communities. Seeds, tubers, and vegetation of submerged aquatic vegetation are energy-rich forage for many waterbirds, especially waterfowl (Krapu and Reinecke 1992). Additionally, submerged aquatic vegetation also provides ideal habitat for many aquatic-macroinvertebrate species that various waterbird species consume (Krapu and Reinecke 1992; Anteau et al. 2011; Anteau 2012).

Relative to *Typha*, many of the displaced emergent species are shorter with much smaller diameter stems, which provides adequate overhead cover for nesting and secretive marsh waterbirds while still allowing movement within the canopy (Kantrud 1986). For example, *Typha* is less preferred by waterbirds than bulrushes, which have smaller diameter stems and lower stem densities that allow swimming and flushing escape (Low 1945; Mack and Flake 1980; Raven et al. 2007) (Fig. 6b). In many cases, dense *Typha* stands quickly fill wetland basins, precluding most waterbird use and reducing the length of time a wetland can exist in the waterfowl-optimal hemi-marsh condition (Kantrud 1986, 1992; Sojda and Solberg 1993; Solberg and Higgins 1993; Linz et al. 1996a, b; Linz and Blixt 1997). While secretive marsh birds are often associated with dense stands of *Typha*, most species require a more varied habitat structure not present in *Typha*-dominated systems (Johnson and Dinsmore 1986; Linz et al. 1997; Rehm and Baldassarre 2007; Hill 2017).

Typha provide abundant forage and den construction material for muskrats (*Ondatra zibethicus*; Fig. 6c), and *Typha* dynamics have been linked to muskrat population trends (Errington 1939; Weller 1988; Kantrud 1992). Additionally, the dense cover of *Typha* provides excellent hiding and thermal cover for white-tailed deer (*Odocoileus virginianus*; Fig. 6d), pheasants (*Phasianus colchicus*), and invasive wild boar (*Sus scrofa*), which helps support their populations in highly agricultural landscapes that may have limited tree and shrub cover (Fritzell 1989; Kantrud 1992; Homan et al. 2000; Homan et al. 2003).

Fishes

The tendency for invasive *Typha* to grow in dense, homogeneous stands and reduce native plant diversity (Frieswyk and Zedler 2007; Wilcox et al. 2008; Tuchman et al. 2009; Lishawa et al. 2010) can negatively affect fish communities (Smokorowski and Pratt 2007; Hagerthey et al. 2014). Diverse plant assemblages and heterogeneous plant growth forms found in native marsh habitats tend to result in increased diversity and species richness of larval (Höök et al. 2001; Tanner et al. 2004), juvenile, and adult fish communities (Tonn and Magnuson 1982), and the increased growth and survival of fishes (Olson et al. 1998). Invasive *Typha* stands contain fewer submergent plant species with highly dissected leaves and fewer floating-leaved plants compared to native marsh areas (Lawrence et al. 2016a), reducing options for cover and foraging for fishes. For example, foraging by ambush predators such as largemouth bass (*Micropterus salmoides*), northern pike (*Esox lucius*), or Florida gar (*Lepisosteus platyrhincus*) may be negatively affected by the increased stem density and reduced heterogeneity of *Typha* stands (Hagerthey et al. 2014; Trebitz and Hoffman 2015).

The conversion of native coastal marsh habitat to a *Typha* monoculture can reduce the utility of these areas as spawning sites for economically important fish species. For example, in the Upper St. Lawrence River, *Typha* invasion replaced native sedge species, thereby reducing northern pike (Fig. 6e) spawning habitat and causing overlap in pike and muskellunge (*Esox masquinongy*) spawning sites (Cooper et al. 2008). Furthermore, the increase in stem density and litter caused by *Typha* can reduce water column dissolved oxygen, making these spawning grounds inhospitable as nursery and rearing areas for larval and juvenile fishes (Bunch et al. 2010; Hagerthey et al. 2014; Bunch et al. 2015). Though dense *Typha* stands can be suboptimal for some fish species, when combined with differences in nutrient levels, Turner et al. (1999) observed higher fish biomass in nutrient-enriched *Typha* areas compared to oligotrophic areas dominated by native plant species in the Everglades.

Invertebrates

Typha invasion can alter aquatic-invertebrate communities (Fig. 6f) by reducing structural complexity as heterogeneous, native marshes are converted to areas dominated by dense, thick-stemmed *Typha* that produces copious litter (Krecker 1939; Farrer and Goldberg 2009; Lawrence et al. 2016a). Macroinvertebrates, however, have been shown to colonize *Typha* litter and often display varied responses to vegetation communities (Nelson et al. 1990b; Batzer 2013; Yozzo and Osgood 2013). In P-enriched areas of the Florida Everglades King and Richardson (2007) concluded that *Typha* growth effected periphyton and the aquatic invertebrates that rely on it as a food source. Lawrence et al. (2016a) found that in Great Lakes coastal wetlands, invasive *Typha* plots had reduced submerged and floating-leaved plant species diversity compared to native marsh plots, which corresponded with a decrease in macroinvertebrate biomass and density. These data suggest that increasing habitat heterogeneity by reducing the abundance of *Typha* (Cardinale et al. 1997) may increase macroinvertebrate biomass, thereby improving habitat for higher trophic levels such as birds (Kostecke et al. 2005). For example, Schummer et al. (2012) found increased macroinvertebrate abundance in dredged ponds within Lake Erie coastal wetlands compared to *Typha*-dominated areas. In addition to homogenizing habitat, the abundant litter produced by *Typha* can result in hypoxia, reducing macroinvertebrate abundance and causing shifts in macroinvertebrate communities (Rose and Crumpton 1996; Christensen and Crumpton 2010). Similar to data for fishes, when *Typha* presence was combined with nutrient differences, McCormick et al. (2004) documented a significant increase in macroinvertebrate densities in P-enriched *Typha* stands compared to unenriched sites when using sweep nets to collect data. However, the same study found the opposite result when using different sampling devices, i.e., Hester Dendy samplers, demonstrating the effects of sampling protocol and challenges in this field of research.

Crayfish seem to show a different pattern in response to *Typha* invasion compared to other invertebrate taxa. For example, in the nutrient-enriched Everglades, *Typha*-dominated plots had the greatest density and biomass of crayfish (*Procambarus fallax*) compared to plots where *Typha* was removed (Hagerthey et al. 2014). Similarly, in Great Lakes coastal wetlands, crayfish (*Orconectes* spp.) abundance was lower in native-marsh sites compared to *Typha*-invaded sites (A. Schrank, unpublished data). It is unknown whether absence of crayfish in native-marsh sites is a result of increased predation by more abundant fish predators or habitat preference by crayfish.

Amphibians

Amphibians are key components of wetland food webs as they uniquely rely on both aquatic and terrestrial habitats within their lifetimes, and transfer a significant quantity of nutrients across the aquatic-terrestrial boundary (Brazner et al. 2007) (Fig. 6g). Amphibians are widely used as bioindicators because many species are sensitive to changes in physical and chemical habitats, including non-native plant species invasions (Mifsud 2014). Dense stands of invasive *Typha* have the potential to negatively affect amphibians by increasing marsh desiccation and reducing and fragmenting habitat for reproduction, larval development, and movement and migration (Meyer 2003; Perez et al. 2013; Mifsud 2014). Although studies of *Typha* effects on amphibians are limited, negative correlations between dense stands of invasive *P. australis* and amphibian species richness have been documented (Meyer 2003; Mifsud 2014). Amphibians are likely unable to move as effectively through dense stems of *P. australis*, and amphibians in *Typha* would be similarly challenged due to the structural similarity. Perez et al. (2013) found that dense stands of *P. australis* slowed larval development of juvenile wood frogs (*Lithobates sylvaticus*), although the mechanism for this was not clear. It has also been suggested that the high carbon:nitrogen:phosphorus ratio and consequent slow decomposition rate of *Typha* litter may negatively affect frog larvae (Stephens et al. 2013). Finally, invaded wetlands are commonly managed via herbicide and/or burning (Linz and Homan 2011; Svedarsky et al. 2016), which can negatively affect amphibians (Russell et al. 1999; Howe et al. 2004).

Pollinators

Bees and other insects play a critical role in pollination and maintaining ecosystem function (Ollerton et al. 2011; Calderone 2012) (Fig. 6h). The importance of wetlands in supporting bee diversity and forage plants has only recently been studied (Smart et al. 2017; Stephenson 2017), and the effects of invasive *Typha* on bee populations are largely unknown. Spread of invasive plants into native habitats has the potential to negatively affect bee populations through reduction in native flower diversity and flower fitness (Larson et al. 2006; Larson et al. 2014). In general, homogenization of habitat caused by invasive species is likely to have the greatest effect on bee species that have narrow and specialized pollen diets (e.g., oligolectic bees). Although bees will readily collect pollen from *Typha* (Smart et al. 2017), *Typha* pollen has limited nutritional value and may be toxic to bees (Schmidt et al. 1989). Honey bees fed *Typha* pollen have reduced survival relative to those fed pollen from other plants (Schmidt et al. 1987). In the Northern Great Plains, beekeepers favor areas with wetlands when selecting locations to keep honey bee colonies for the summer, presumably because wetlands support flowering plants throughout the growing season and provide water sources to foraging bees (Gallant et al. 2014; Otto et al. 2016).

Nutrients

Typha invasion magnifies N and P availability and biogeochemical cycling in wetlands (Fig. 7a). Feedbacks between enhanced nutrient availability and *Typha* invasion can complicate interpretation of field observations when evaluating cause and effect of this pattern. Most studies point to elevated nutrients facilitating *Typha* invasion, which then leads to further changes in ecosystem nutrient cycling due to the characteristics of *Typha* (Farrer and Goldberg 2009; Currie et al. 2014).

Typha invasion is associated with increased sediment deposition in wetlands, which accelerates inputs of sediment-attached N and P. *Typha domingensis* and

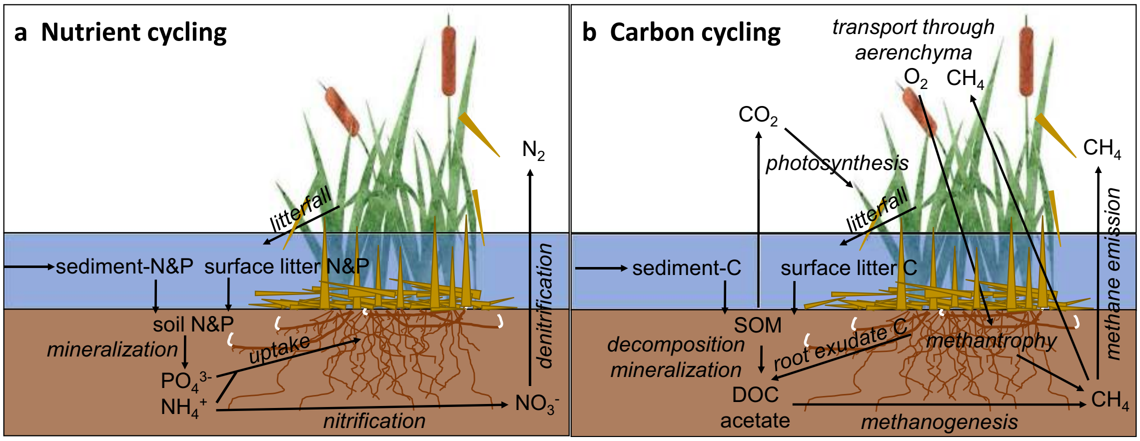

Fig. 7 *Typha* affects many biogeochemical processes including **a** nutrient and **b** carbon cycling

T. angustifolia both increase sedimentation and associated nutrient deposition (Horppila and Nurminen 2001; Anderson and Mitsch 2006). *Typha* × *glauca* is also associated with areas of greater sedimentation in wetlands (Werner and Zedler 2002). Both increased deposition and the accumulated organic matter left after litter decomposition can raise the soil surface relative to the water table (Kirschner et al. 2001), resulting in further alteration of nutrient cycles.

Invasive *T.* × *glauca* amplifies internal nutrient cycling in wetland ecosystems (Currie et al. 2014). Much higher concentrations of extractable nitrate, ammonium, and phosphate are commonly found in soils of *T.* × *glauca* patches in marshes it has invaded (Angeloni et al. 2006; Farrer and Goldberg 2009; Tuchman et al. 2009; Lishawa et al. 2010; Geddes et al. 2014; Lishawa et al. 2014). *Typha* × *glauca* has greater nutrient uptake rates than native wetland plants (Larkin et al. 2012b), leading to increases in N and P concentrations (Woo and Zedler 2002) and standing stock (Boers and Zedler 2008) in *T.* × *glauca* after nutrient fertilization. In the Everglades, *T. domingensis* is capable of accessing legacy P in nutrient-enriched soils even after P input into the system has been decreased (Noe and Childers 2007; Richardson et al. 2008b). Increases in above-ground plant nutrient uptake and concentrations are greater for invading *T. domingensis* than for native sedges in the Everglades, but no differences in nutrient resorption proficiency typically occur (Davis 1991; Newman et al. 1996; Noe et al. 2001; Childers et al. 2003; Miao 2004; Noe and Childers 2007). The elevated N concentrations and greater biomass production of *T.* × *glauca* also result in greater ecosystem N retention (Currie et al. 2014). Yet, when invasive *Typha* is treated with herbicide to meet management objectives, decreased plant demand results in increased soil inorganic nutrient availability (Lawrence et al. 2016b; Elgersma et al. 2017), which may set the stage for reinvasion, algal blooms, or export of nutrients to adjacent aquatic systems. Nutrient release is of particular concern in ecosystems such as the Everglades, where downstream ecosystems are oligotrophic.

Typha invasion also affects soil-nutrient biogeochemistry through its production of large amounts of detritus. Only the litter of *T.* × *glauca*, and not live plants, increased soil N mineralization rates and extractable ammonium concentrations in a transplant experiment (Farrer and Goldberg 2009). Phosphorus enrichment, which led to *T. domingensis* invasion, also stimulated soil P availability (Rejmánková 2001) and N mineralization (White and Reddy 2000). *Typha* × *glauca* was able to utilize N from its own litter more than co-occurring native plants could (Larkin et al. 2012b). *Typha domingensis* litter immobilizes more N and P during decomposition than native sedges (Davis 1991). Nutrient and litter manipulations suggested that the physical structure of *T. angustifolia* litter was a key factor in nutrient cycling, rather than decomposition (Jordan et al. 1989; Jordan et al. 1990). In a brackish tidal marsh, *T. angustifolia* litter minimized the stimulation of sediment N and P concentrations in response to experimental fertilization through some physical mechanism, perhaps shading that cooled the soil (Jordan et al. 1989).

Finally, soil denitrification is altered by *Typha* invasion. The soil under *T.* × *glauca* has greater denitrification gene diversity but not gene abundance (Angeloni et al. 2006; Geddes et al. 2014). Greater denitrification potential rates are associated with *Typha* in constructed wastewater treatment wetlands (Chen et al. 2014) and in natural wetlands invaded by *T.* × *glauca*, although there are variable patterns of change in denitrification with age since invasion (Geddes et al. 2014; Lishawa et al. 2014). Because denitrification is a valuable ecosystem service that removes reactive N from the biosphere and improves water quality, enhanced rates of denitrification that result from *Typha* invasion should be weighed against other ecosystem services that may be impaired by invasion (Lishawa et al. 2014).

Carbon and Greenhouse Gases

Despite extensive work investigating carbon (C) cycling associated with wetland plant communities, few studies have explicitly examined effects of *Typha* invasion. Understanding invasion impacts on C-related processes is challenging because *Typha* invasion and the wetland C cycle are both sensitive to changes in hydrology and nutrient additions, making it difficult to establish causality in observational studies. For example, nutrient additions can simultaneously facilitate *Typha* invasion and strongly increase soil organic matter (SOM) (Martina et al. 2014), creating the impression that *Typha* increases SOM. Further, the relative impact of invasion is also a function of the species that are replaced. Here, we draw on studies that explicitly examined *Typha* invasion impacts on C-related processes, as well as those that addressed the underlying mechanisms associated with *Typha* invasion (Fig. 7b).

Due to traits associated with resource acquisition (i.e., growing tall, producing large amounts of aboveground and root belowground biomass), plant invasions tend to enrich SOM and increase C storage in plant, litter, and microbial biomass pools (Liao et al. 2008; Ehrenfeld 2010; Vilà et al. 2011). *Typha* conforms to this syndrome, as *Typha*-invaded stands tend to be more productive and taller than the species they replace. In the LGL, *T.* × *glauca* produces ~2 times as much aboveground biomass as the native sedge- and rush-dominated communities it typically replaces (Lawrence et al. 2017), and *T. domingensis* in the Everglades tends to be ~1.5 times taller than the native sawgrass it outcompetes (Miao and Sklar 1998). Since *Typha*'s high primary productivity promotes CO_2 uptake while anoxic soils slow down CO_2 release via decomposition and other heterotrophic processes, C tends to accumulate in surface litter and soils in *Typha*-invaded wetlands; this has been documented in paleoecological studies of *Typha*-dominated marsh sites (e.g., Finkelstein et al. 2005). Surface litter can accumulate rapidly when *Typha* invades due to high aboveground biomass production coupled with relatively slow decomposition rates, largely due to a prolonged standing dead phase (Davis and van der Valk 1978; Vaccaro et al. 2009). For example, litter mass doubled within 10 years of *Typha* invasion in a Lake Michigan coastal wetland (Mitchell et al. 2011). Standing dead and surface litter can account for one-half to two-thirds (600–2500 g litter m^{-2}) of the total aboveground biomass in established *Typha* stands (Childers et al. 2003; Vaccaro et al. 2009), representing a large C pool. High rates of nutrient resorption also promote C storage; by examining three co-occurring wetland invaders, Martina et al. (2014) demonstrated that it is the combination of a large quantity and low quality of litter that promotes C accretion under *Typha*. In a mesocosm experiment, Lawrence et al. (2017) found that the percentage of soil C doubled after 10 years of invasion. Although feedbacks between hydrology, nutrients, and plant dominance may confound interpretations from field surveys, across 14 northern Great Lakes wetlands, *Typha*-dominated stands had greater SOM (14% vs. 5%) and deeper surface organic horizons (16 cm vs. 3 cm) than uninvaded reference stands (Lishawa et al. 2010). Using a space-for-time substitution approach in a Lake Huron wetland complex, Mitchell et al. (2011) demonstrated that SOM content increased with time since *Typha* invasion.

Typha invasion alters CH_4 emission from wetlands. A primary mechanism by which plants regulate CH_4 emissions from wetlands is by providing the methanogen community with C substrates for anaerobic respiration (Sutton-Grier and Megonigal 2011). Biomass turnover and root exudation provide microbial communities with labile C, with many studies observing greater CH_4 emissions with greater *Typha* biomass production (Whiting and Chanton 1993; Updegraff et al. 2001; Cheng et al. 2007; Zhang et al. 2010; Kao-Kniffin et al. 2011). Similarly, 10 years after experimental *Typha* invasion, Lawrence et al. (2017) observed greater CH_4 emissions from *Typha*-dominated vs. *Carex*/*Schoenoplectus*-dominated mesocosms, with aboveground biomass and soil C positively associated with CH_4 emissions. In addition to providing abundant C substrates, spongy, aerenchymatous *Typha* tissues also provides a pathway for CH_4 produced in the underlying anoxic sediment to bypass oxidized surface sediments and waters, thereby increasing CH_4 emissions. McInerney and Helton (2016) observed greater CH_4 emissions when *Typha* was present compared to unvegetated controls in constructed wetlands. *Typha*-mediated CH_4 emissions accounted for >50% of CH_4 leaving the littoral zone of a dense *Typha* pond (Sebacher et al. 1985). Yavitt and Knapp (1995) and Yavitt and Knapp (1998) suggested that *Typha* acts as a capacitor, filling with CH_4 at night and emitting during the day. This is supported by Windham-Myers et al. (2018), who observed 2-times greater CH_4 emissions during the daytime than night in a *Typha*-dominated marsh.

Aerenchyma may also oxygenate the rhizosphere, potentially shifting microbial composition and activity and promoting CH_4 oxidation that could reduce net emissions (Carmichael et al. 2014). This mechanism may be at least partially responsible for observations of negative (or no) relationships between biomass and CH_4 emissions. Across nine wetland plant species, Kao-Kniffin et al. (2010) examined relationships among CH_4 emission, biomass, and microbial communities and found that *Typha* had one of the lowest rates of emissions, and in general, CH_4 emissions decreased with greater plant biomass. Within an impounded restored freshwater wetland in California, Windham-Myers et al. (2018) observed higher CH_4 emissions from *Typha*-dominated vs. *Schoenoplectus*-dominated plots, despite *Typha* plots having lower aboveground-biomass. In a parallel study, He et al. (2015) observed lower acetoclastic methanogenesis activity via *Methanosarcina* in *Typha* rhizomes than *Schoenoplectus*.

Kao-Kniffin et al. (2011) showed that an increase in CH_4-producing archaea isolated from the rhizosphere of *Typha* was associated with enhanced plant biomass from CO_2-stimulated roots, and that CO_2-enrichment (700 ppm) elevated CH_4 emissions (148%).

Agriculture

The proliferation of *Typha* has impacted industrial-scale agriculture, small-scale production, and subsistence farming across the globe. *Typha* can affect a variety of agricultural sectors directly by competing with water-submerged crops such as wild rice, taro, and water chestnut (Muenscher 1955; Smith et al. 1977; Hawaii Invasive Species Council 2008; Minnesota Department of Natural Resources 2008; Pillsbury and McGuire 2009; Kumar 2011), or indirectly by altering sediment characteristics, salinity, plant communities, water quality, and water availability (Otis 1914; Glenn et al. 1995; Holm et al. 1997; Werner and Zedler 2002). However, *Typha* is not a major weed in large-scale production where herbicides, land preparation, and water management are used in integrated weed management plans (Mahajan et al. 2014).

Typha can act as a physical barrier to water flow and obstruct rivers, irrigation canals, farm ponds, reservoirs, and drainage ditches (Timmons et al. 1963; Hamdoun and El Tigani 1977; Kumar 2011; Rodenburg and Johnson 2013; Sabo et al. 2016). For example, after dam and canal installation in Nigeria, the expansion of *T. domingensis* caused river blockage that further reduced flooding, negatively affecting recession agriculture (Ringim et al. 2015). Additionally, impeded water flow combined with monotypic stands of *Typha* can interfere with fishing by obstructing travel and decreasing quality of fisheries (Morton 1975; Holm et al. 1997; Ringim et al. 2015). In India, about 40% of freshwater lakes are rendered unsuitable for pisciculture because of invasion by aquatic weeds, including *Typha* (Kumar 2011). *Typha* can also capture blowing snow in agricultural fields and result in the ponding of snow-melt water that can delay or prevent farmers from planting in these areas. To combat this effect, farmers will often burn *Typha* stands in the fall or early winter to remove standing vegetation (Renton et al. 2015).

Typha can also impact livestock forage, health, and pastureland. *Typha* provides low quality forage in terms of nutrient content and palatability (Timmons et al. 1963; Kirby et al. 2002). Although generally edible, a few cases have implicated *Typha* in poisoning horses (Kingsbury 1964), cattle (Hurst 1942), and humans (Woodcock 1925). Large stands of *Typha* can harbor increased disease vectors, such as mosquitoes, snails and parasitic worms, potentially putting livestock and humans at greater disease risk (Cantrell 1981; Cogels et al. 1997; Pfukenyi et al. 2005; Pope et al. 2005; Salako et al. 2016). In the case of traditional grazing in Nigeria, large swaths of *Typha* have reduced the amount of available dry-season pasture (Degeorges and Reilly 2006).

Typha-dominated wetlands provide habitat for wildlife species that impact agriculture. *Typha* has been found in feral hog diets and may help sustain hog populations when agricultural crops are not available (Bratton 1974; Herrero et al. 2004). Extensive swaths of *Typha* are roosting habitat for flocks of grain-eating birds. Weavers (Ploceidae) throughout Europe, Asia, and Africa impact rice (*Oryza*), wheat (*Triticum*), millet (*Panicum*), and sorghum (*Sorghum*) (Tanko 2007; Borokoni and Babalola 2012; Ringim et al. 2015). In South America, Dickcissels (Cardinalidae) feed on cereals such as rice and sorghum (Basili and Temple 1999). In North America, blackbirds (Icteridae) forage on sunflower (*Helianthus*) (Fig. 6i), corn (*Zea*), and rice (Meanley 1965; Dolbeer 1990; Glahn et al. 1994; Linz et al. 2011; Peer and Abernathy 2017). Interestingly, in California, limited area of fresh, green *Typha* growth has prompted the tricolored blackbird (*Agelaius tricolor*) to nest in agricultural fields, which requires producer buyouts or altered haying schedules to protect this endangered species (Meese 2006; Graves et al. 2013; Holyoak et al. 2014).

Case Study: *Typha*, Blackbirds, and Crop Damage in the PPR

Research on management of *Typha*-dominated wetlands and influences on wildlife and concurrent agricultural damage has mainly been carried out in the depressional wetlands of the PPR. Three blackbird species, red-winged blackbirds (*Agelaius phoeniceus* L.), common grackles (*Quiscalus quiscula* L.), and yellow-headed blackbirds (*Xanthocephalus xanthocephalus* Bonaparte) cause significant economic damage to crops, especially sunflower (Fig. 6i) and corn (Peer et al. 2003; Klosterman et al. 2013; Shwiff et al. 2017). Their combined post-breeding population, estimated at 75 million, prefers *Typha*-dominated semi-permanent wetlands as roost sites during late summer due to the increased protection provided by dense *Typha* stands (Peer et al. 2003). Flocks emanate from these safe havens to forage in nearby crops (Ralston et al. 2007), especially corn and sunflower (Klosterman et al. 2013). In 2009 and 2010, Klosterman et al. (2013) estimated that blackbirds annually damaged $1.3 million USD and $3.5 million USD of ripening corn and sunflower in North Dakota, respectively. Managing the areal coverage of *Typha* to reduce the availability of blackbird habitat is one method of dispersing large blackbird concentrations to many smaller roosts (Linz et al. 1995; Linz and Homan 2011), thereby reducing the severity of localized damage (Leitch et al. 1997) while improving wetland habitat (Linz 1992; Solberg and Higgins 1993; Linz and Homan 2011; Linz and Klug 2017).

Changing climate and hydrology may result in earlier and more robust spring growth of *Typha,* which then persists as live vegetation into autumn. Earlier-developing *Typha* would provide enhanced nesting habitat for blackbirds that are correspondingly arriving earlier on nesting grounds (Torti and Dunn 2005; Forcey and Thogmartin 2017). Dense *Typha* stands, combined with an adequate moisture regime, provide habitat for late-migrating blackbirds foraging on late-maturing crop varieties, especially sunflower and corn, which are supplanting small grains in the northern Great Plains (Klosterman et al. 2013). Harvested row crops, in combination with greater areal coverage of *Typha* within roost sites, could provide superior stopover habitats for blackbirds during both fall and spring migration in the US and Canada (Homan et al. 2006; Hagy et al. 2008; Galle et al. 2009). The relationships between climate change, hydrology, evolving wetland habitat, cold-tolerant crop varieties, blackbird migration, and *Typha* could well change crop damage distribution and intensity across agricultural areas of North America (Melillo et al. 2014; Forcey and Thogmartin 2017; Klug 2017).

Section 4: Ecosystem Services

Customary and Traditional Uses

Typha has long been important to indigenous peoples from various regions of the world, who have relied on each part of the plant for an assortment of uses ranging from food and medicine to production of goods (Morton 1975; Mitich 2000). Different portions of the plant are eaten raw or prepared in various ways (Fig. 8a), and flour made from *Typha* rhizomes has comparable protein content to corn, rice, and wheat. *Typha* can also be a source of feed and bedding material for livestock, albeit palatability is lower than other forage (Morton 1975; Mitich 2000; Ciria et al. 2005). Several cultures have developed medicinal applications for *Typha* ranging from treatment of burns, to use as an astringent, diuretic or wound wrapping, to a remedy for several afflictions. Plant parts have been used to produce goods such as woven baskets and mats, rope and twine, paper, sandals, fans, torches, spear handles, toys, and boats. In fact, harvesting *T. domingensis* for such goods may increase plant diversity in central Mexican wetlands (Hall et al. 2008). For some indigenous nations and communities, *Typha* remains an important food and medicinal plant and is regarded alongside other plants and animals as family or kin (Reo and Ogden 2018). In the LGL, Anishinaabe families continue to gather *Typha* for a wide variety of uses, primarily as a food item in the early spring (Fig. 8a). Reo and Ogden (2018) described a workshop in which elders taught youth how to harvest and prepare *Typha*. At this same workshop, participants successfully used the invasive *T.* × *glauca* to prepare traditional and new recipes as a way of enacting and discussing what Anishinaabe-*Typha* relations might look like in an era of invasive species.

Typha biomass also shows promise for use as building material and insulation and has shown potential for production of bio-adhesives (Morton 1975; Mitich 2000; Colbers et al. 2017). *Typha* 'seed fluff' has been used to stuff pillows, cushions, and mattresses, as kindling for lighting fires (Fig. 8b), and as fill for life-jackets during World War II (Morton 1975; Mitich 2000). More recently, Yu et al. (2017) suggested that porous C extracted from *Typha* could be used as an adsorbent and supercapacitor.

Bioremediation

Bioremediation is a soil and water management technique that uses biological organisms to break down and remove contaminants, including industrial, agricultural, and urban runoff (Gottschall et al. 2007; Pietro and Ivanoff 2015), wastewater (Vymazal 2013; Bhatia and Goyal 2014; Vymazal 2014), and mine waste (Groudev et al. 2008). Natural and constructed wetlands are widely used for various types of bioremediation, including phytoremediation (plants), microbial bioremediation (microorganisms), and mycoremediation (fungi) (Stottmeister et al. 2003; Marchand et al. 2010; Headley and Tanner 2012; Biswas 2015; Truu et al. 2015). *Typha*, in particular, has been associated with successful phytoremediation efforts, largely for metals and nutrients, due in large part to its rapid growth rates, capacity for elemental uptake, tolerance of contaminated environments, and limited translocation of

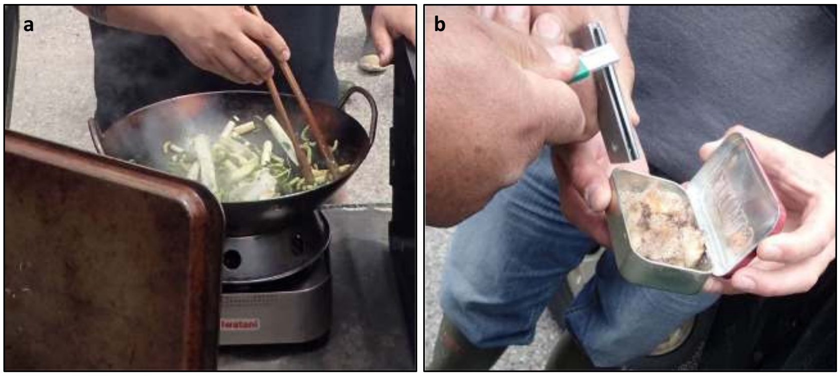

Fig. 8 Indigenous uses of *Typha* for **a**) cooking and **b**) as part of a fire starter kit. Pictures taken at a workshop on Anishinaabe-*Typha* relationships (Reo and Ogden 2018)

harmful elements from roots to aboveground biomass (Coon et al. 2000; Hegazy et al. 2011; Leto et al. 2013; Lyubenova et al. 2013; Gomes et al. 2014; Mufarrege et al. 2014; Pandey et al. 2014; Lominchar et al. 2015; Bonanno and Cirelli 2017).

In many parts of North America where *Typha* is considered invasive, nutrient removal (mainly N and P) is important. The high biomass, growth rate, and clonal expansion rates of *Typha* result in stands of *Typha* acting as N and P sinks; thus, *Typha* stands may be useful for phytoremediation efforts (Coon et al. 2000; Woo and Zedler 2002; Gottschall et al. 2007; Gebremariam and Beutel 2008; Varnell et al. 2010; Grosshans et al. 2013; Chen and Vaughan 2014; Grosshans 2014; Grosshans et al. 2014; Jeke et al. 2015; Berry et al. 2017). Chen and Vaughan (2014), however, caution that prolonged inundation may affect the ability of *Typha*-dominated systems to remove P. In a six-years study of a *Typha*-dominated wetland that served as a filter for a lotic system, Coon et al. (2000) reported that the wetland removed 28% of P inputs. Gottschall et al. (2007) reported that a *Typha*-dominated wetland removed up to 9% of total Kjeldahl N (sum of organic nitrogen, ammonia, and ammonium), 21% of ammonium, and 5% of total P from livestock wastewater. Jeke et al. (2015) determined that harvesting of *Typha* biomass when aboveground nutrient concentrations are at their peak results in removal of 4% of total N and 3% of total P from municipal biosolids. Grosshans (2014) and Grosshans et al. (2013, 2014) evaluated harvesting of *Typha* biomass as a watershed remediation practice to reduce P loading to downstream Lake Winnipeg, resulting in 1–2 kg P per metric ton of biomass per year removed through harvested biomass in late summer. Gebremariam and Beutel (2008) showed that *Typha* was effective for treating nitrate-dominated wastewaters, with removal rates ranging up 400–500 mg N m^{-2} d^{-1} when nitrate levels exceeded 15 mg N L^{-1}.

Many studies and reviews have indicated that various species of *Typha* show promise for phytoremediation of metals in wastewaters due to their ability to bioaccumulate metals such Cd, Cr, Fe, Hg, Ni, Pb, and Zn (Demirezen and Aksoy 2004; Maddison et al. 2009; Marchand et al. 2010; Hegazy et al. 2011; Mojiri et al. 2013; Bhatia and Goyal 2014; Sultana et al. 2014; Lominchar et al. 2015; Bonanno and Cirelli 2017). In a review of metal removal in constructed wetlands, Marchand et al. (2010) summarized removal rates for monocultures of *Typha* ranging from 48 to 99% for Cd, Cr, Fe, Ni, Pb, and Zn; moreover, Sultana et al. (2014) found Cr removal efficiency rates for *Typha* ranging from 50 to 95%. Bhatia and Goyal (2014) reported that macrophytes including *Typha* accumulated 2049–6648 μg metal per gram of dry plant biomass and (Mojiri et al. 2013) reported that, under optimal conditions, *T. domingensis* removed 0.97, 0.47, and 0.37 mg kg^{-1} of Pb, Ni, and Cd, respectively. Various studies also reported high Hg bioaccumulation factors for *Typha* (Gomes et al. 2014; Lominchar et al. 2015; Bonanno and Cirelli 2017). In addition, phytoabsorption by *Typha* has been suggested for treating de-icing salts in road ditches (Morteau et al. 2015).

Bioremediation Case Study: South Florida Stormwater Treatment Areas

In the 1990s, the State of Florida implemented a strategy to reduce total P loads from nutrient-rich stormwater runoff into the Everglades ecosystem by constructing bioremediation treatment wetlands, or Stormwater Treatment Areas (STAs) (Chimney and Goforth 2001). Currently, more than 23,000 ha have been converted to STAs where plants such as *Typha* uptake P (Chimney 2018). The P is stored in plant biomass and soils (as partially decomposed plant material), resulting in lower P loads transported downstream to the Everglades. In 2017 alone, it was estimated that STAs reduced total P loads and concentrations by nearly 85%, preventing >100 metric tons of P from flowing into the Everglades (Chimney 2018). Furthermore, it has been estimated that over the 23 years since their establishment, the STAs have retained approximately 2300 metric tons of total P that otherwise would have been transferred to the Everglades (Chimney 2018).

Establishment of the STAs has provided ample opportunity for researchers to examine the effectiveness of treatment wetlands and wetland vegetation (e.g., *Typha*) for nutrient remediation in a subtropical region. Bhomia et al. (2015) and Pietro and Ivanoff (2015) examined soil and P accretion rates and P removal efficiency, while Chimney and Pietro (2006) and Dierberg and DeBusk (2008) assessed plant decomposition and particulate P. Other researchers have examined topics such as annual P loading, storage and removal, wetland restoration, mass balance models, and hydrology (e.g., Newman and Pietro 2001; Juston and DeBusk 2006, 2011; Moustafa et al. 2011; Juston et al. 2013; Chen et al. 2015). Chimney and Pietro (2006) reported low decomposition rates for *Typha* compared to other plant species, suggesting that *Typha*-dominated wetlands would be ideal for retaining P; however, various species of submerged aquatic vegetation may remove greater amounts of soluble P than *Typha*. To date, research from the south Florida STAs and elsewhere (see references in Kadlec and Wallace 2009) indicates that wetlands and their associated plant communities, including *Typha*, can be effective at bioremediation.

Biomass Harvest

Management of *Typha* often includes removal of biomass (Fig. 9d), and recent research and reviews have examined the potential use of this biomass as a biofuel crop (Dubbe et al. 1988; Ciria et al. 2005; Wang et al. 2011; Grosshans et al. 2013; Grosshans 2014; Grosshans et al. 2014; Elhaak et al. 2015; Rahman et al. 2015; Svedarsky et al. 2016; Ahmad

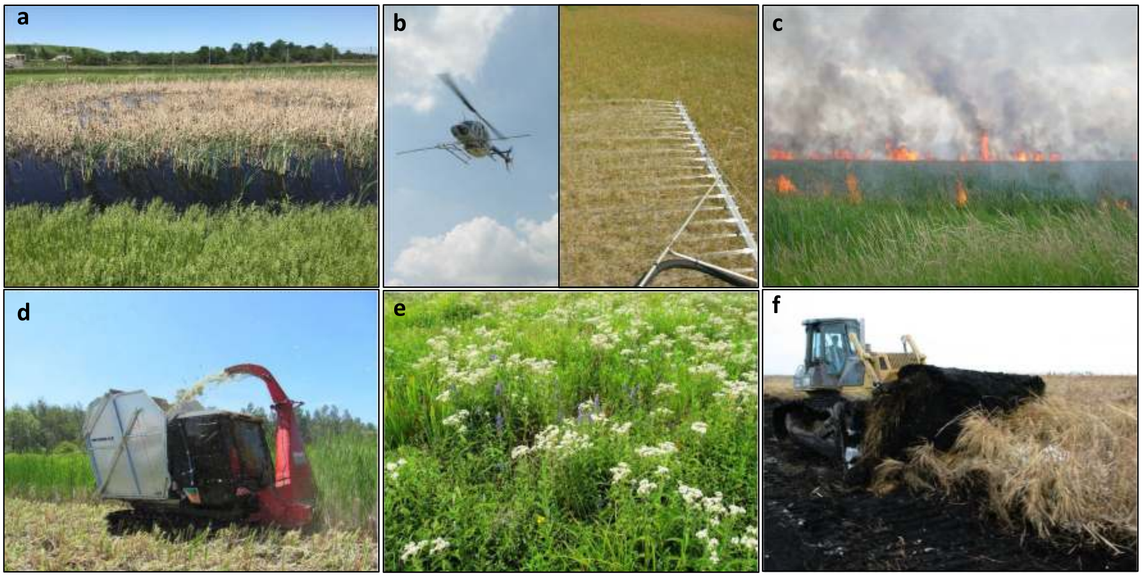

Fig. 9 Various examples of *Typha* management techniques: **a** water-level manipulation at an experimental wetland at the U.S. Geological Survey, Northern Prairie Wildlife Research Center in the Prairie Pothole Region-note that flooding killed most of the *Typha* in the wetland, but some rhizomes near the wetland edge were able to send up new ramets that require additional treatments; **b** aerial application of herbicide to manage *Typha* within the northern Everglades; **c** prescribed burn of a *Typha* marsh at Agassiz National Wildlife Refuge, Minnesota, USA in 2006 where flame heights reached >9 m; **d** harvesting *Typha* × *glauca* with a biomass harvester designed for wetland use (Loglogic Softrak, Devon England, U.K.) in Cheboygan Marsh, Michigan, USA; **e** re-vegetation to restore floristic diversity at Cowles Bog Wetland Complex in Indiana Dunes National Lakeshore; and **f**) removal of *Typha* biomass and sediment to restore wetland habitat in the Prairie Pothole Region

et al. 2017; Berry et al. 2017; Rebaque et al. 2017; Carson et al. 2018). In a review of *Typha* management in the northern Great Plains, Svedarsky et al. (2016) highlighted numerous advantages that *Typha* has over other sources of biomass, including that it occurs in wetland areas that are not suitable for conventional agriculture, it is quickly renewable, it is a C-neutral resource, tillage and replanting are typically not required, and harvesting *Typha* can improve wetland habitats. Rahman et al. (2015) demonstrated that byproducts of fresh *Typha* biomass can be used directly in the production of ethanol, as well as indirectly through the cultivation of microalgae that can then be used to produce ethanol. Moreover, Berry et al. (2017) suggested that, in addition to providing a biofuel feedstock and reducing downstream nutrient loading, harvesting of plant (e.g., *Typha*) biomass from surface-water retention systems provided additional income for landowners through various revenue streams.

A number of studies have examined the thermal characteristics of *Typha*, and identified optimal processing methods for ethanol production. Studies show *T. latifolia* holds great promise as a bioenergy feedstock due to its structural cell-wall polysaccharides (Rebaque et al. 2017), high yields, thermal properties (Ciria et al. 2005), and favorable kinetic and thermodynamic properties (Ahmad et al. 2017). In a study examining *T. latifolia* as a potential biofuel alternative to petroleum, Aysu et al. (2012) determined conversion percentages from supercritical gas extraction that ranged from roughly 55–70%, values comparable to other plants such as *Phalaris arundinacea* (reed canarygrass) (52–73%) and *Arundo donax* (giant reed) (40–82%) (Aysu 2012; Aysu and Küçük 2013). Carson et al. (2018) quantified *Typha*'s potential as a feedstock for biogas production in anaerobic digesters and determined that untreated *Typha* was a suitable material for use in mixed source biomass digesters.

A comprehensive study was conducted at Netley-Libau Marsh at Lake Winnipeg, Canada, to assess the feasibility of annual biomass (including *Typha*) harvesting for nutrient bioremediation and biofuel production (Cicek et al. 2006; Grosshans 2014). Annual biomass harvesting would result in the removal of ~1.0–1.4 kt of total N and 188–227 tons of total P from inflows from the Red River, which enter Lake Winnipeg through Netley-Libau Marsh (Cicek et al. 2006). Cicek et al. (2006) also examined the efficacy of various bioenergy production technologies and concluded that they could produce 1.75–4.71 MW of power, in addition to the added benefit of usable, cogenerated heat. Grosshans (2014) estimated that harvesting *Typha* biomass resulted in 15–20 tons dry mass ha^{-1}, effectively removing 30–60 kg P ha^{-1} year^{-1}. Moreover, compressed *Typha* fuel pellets produced heat similar to commercial wood pellets, with values ranging from 16–20 MJ kg^{-1} (Grosshans et al. 2013; Grosshans 2014; Grosshans et al. 2014; Carson et al. 2018). Grosshans (2014) noted that further exploration of economic factors is required to assess feasibility of biomass harvest for nutrient removal and biofuel feedstock, and that harvesting *Typha* for multiple uses (e.g., nutrient capture, bioenergy, habitat management, C offsets, biochar) likely would be required to make the process economically viable. Grosshans et al. (2013, 2014) subsequently implemented *Typha* harvesting at an applied scale in a managed wetland utilized for water retention in the Lake Winnipeg Watershed in Manitoba, Canada. This work demonstrated that managed *Typha* wetlands utilized for water retention provide a suite of stacked benefits in addition to flood water storage: reduced nutrient loading, enhanced wildlife habitat and biodiversity, and sustainable biomass for renewable energy and bioproducts. The 500-ha Pelly's Lake engineered wetland provides 148 ha-m of controlled water storage and has removed over 5 metric tons of P through *Typha* harvest management.

Section 5: Management and Restoration

> *"In theory, there is no difference between theory and practice. But in practice, there is."*
> -Yogi Berra

Control of *Typha* has long been a wetland management concern. Early approaches involved herbicide treatments and water-level manipulations (Steenis et al. 1959; Harris and Marshall 1963). Later, studies tested hand-cutting, mowing, crushing, cultivation, scraping, herbicides, explosives, fire, altering salinity levels, flooding, and drought (Nelson and Dietz 1966; Linde et al. 1976; Beule 1979). On-going studies continue testing various treatments to control *Typha* (Mallik and Wein 1986; Comes and Kelley 1989; Kostecke et al. 2004; Asamoah and Bork 2010; Linz and Homan 2011; Rodgers and Black 2012; Hagerthey et al. 2014). Controlling *Typha* with mechanical or chemical methods alone is rarely successful because of the large rhizome system that allows *Typha* to regenerate quickly (Tu et al. 2001; Svedarsky et al. 2016). Regardless of management technique employed, multiple actions are typically needed to control *Typha*, and hydrology and timing relative to *Typha*'s life history should be considered (Linde et al. 1976; Beule 1979; Gleason et al. 2012; Wilcox et al. 2018). Moreover, the effects of successful treatments often are short-lived, and active management and repeated treatments likely will be required. The goal of this section is to provide a general overview of various management techniques; existing reviews on *Typha* management provide considerably more detail on control strategies, including Apfelbaum (1985), Sojda and Solberg (1993), and more recently, Svedarsky et al. (2016).

Water-Level Manipulation

Aquatic plants vary in their response to water depth, and it has been suggested that *Typha* vigor can be inhibited when water depth exceeds tolerable levels of 1 m (Linde et al. 1976; Beule 1979; Grace and Wetzel 1982a; Grace 1989; Waters and Shay 1990; Sojda and Solberg 1993; van der Valk 1994; Chen et al. 2010) (Fig. 9a). *Typha* also has been shown to be sensitive to drought (Nelson and Dietz 1966; van der Valk and Davis 1980; Li et al. 2004; Asamoah and Bork 2010). Consequently, water-level manipulation has the potential to control *Typha* via flooding or desiccating substrates. However, water-level manipulations, both draining and flooding, appear to be most effective when coupled with other management techniques such as burning or cutting (e.g., Nelson and Dietz 1966; Mallik and Wein 1986; Ball 1990). In wetlands with organic soils, extensive draining causes an increase in inorganic nutrients, as well as increased fire risk, potentially thus exacerbating *Typha* invasion (Newman et al. 1998; Smith et al. 2003).

Herbicide Management

Herbicides used to chemically control *Typha* include 2,4-dichlorophenoxyacetic acid (2,4-D) (Steenis et al. 1959; Corns and Gupta 1971), glyphosate (Schimming et al. 1987; Messersmith et al. 1992; Solberg and Higgins 1993; Linz and Homan 2011), imazapyr (Foloni and Pitelli 2005), and imazamox (Rodgers and Black 2012). Each of these herbicides has commercially available formulations labeled by the US Environmental Protection Agency for aquatic use. All these herbicides are classified as systemic (absorbed and translocated throughout the plant) and are considered non-selective (kill or damage all plants), although selective control has been reported for imazamox applied at low rates (Rodgers and Black 2012). Applications of these herbicides are typically carried out as foliar treatments by ground applicators using tank sprayers, but large treatments can be performed using aircraft (Sojda and Solberg 1993; Thompson et al. 2010; Linz and Homan 2011; Newman et al. 2017) (Fig. 9b) or smaller, more targeted treatments can be applied by hand-wicking stems (Wilcox et al. 2018). Herbicide treatment efficacy is reportedly season-dependent, with the most effective control achieved in late summer months when *Typha* are actively growing and transporting carbohydrates to their rhizomes (Linz and Homan 2011).

Excess nutrients are one of the key drivers of *Typha* invasion (Woo and Zedler 2002; Larkin et al. 2012b), and increasing nutrient availability creates conditions more suitable for re-invasion. Hagerthey et al. (2014) found that total P in the flocculant and soil layers were elevated in herbicide-treated and burned Everglades *Typha* marshes compared to untreated controls. Similar findings of increased pore-water and plant-available N and P were observed in wetlands that were glyphosate-treated to control *T.* × *glauca* (Lawrence et al. 2016b). Thus, application of herbicide may provide short-term control of *Typha* but ultimately create conditions for more aggressive re-invasion.

Development of herbicide resistance in *Typha* has the potential to occur, particularly when using reduced herbicide application rates (Neve and Powles 2005). Restoration practitioners utilizing this approach should include an herbicide resistance management program in their management plan (Norsworthy et al. 2012). Zheng et al. (2017) found absorption of the herbicide glyphosate is four-times greater for native *T. latifolia* than *T.* × *glauca*, suggesting herbicide application could be causing resistance in the hybrid *T.* × *glauca*, and could ultimately aid the spread of the more glyphosate-resistant hybrid while eliminating native species.

Burning

Prescribed fire is a broadly used technique for controlling invasive plants such as *Typha* (Beule 1979; Sojda and Solberg 1993; Ponzio et al. 2004; Gleason et al. 2012; Svedarsky et al. 2016) (Fig. 9c). Studies have shown that *T.* × *glauca* cover can be reduced immediately after burns, but can recover rapidly due to limited belowground effects of fire (Smith and Kadlec 1985; Gleason et al. 2012). In contrast, fire has been shown to favor *T. domingensis* by creating openings in the landscape and increasing bioavailable P (Smith and Newman 2001); fire can temporarily increase *T. domingensis* dominance over native species for 1–2 years post-fire (Ponzio et al. 2004). Therefore, the efficacy of fire for controlling *Typha* is highly variable, and results are often best when combined with other management techniques (e.g., Mallik and Wein 1986; Kostecke et al. 2004). A critical factor for implementing fires in wetland systems is the ability to manipulate water levels; if a site cannot be sufficiently dried, the probability of an effective fire is reduced (Gleason et al. 2012). Fire also eliminates the dense litter layer, which can facilitate re-establishment by native species but also reinvasion by *Typha*.

Physical Disturbance

Physical disturbances such as grazing, mowing, disking, shearing, crushing, and scraping are commonly used to control *Typha* (Beule 1979; Murkin and Ward 1980; Schultz 1987; Ball 1990; Sojda and Solberg 1993; Payne 1998; Wilcox et al. 2018). Weed-cutting boats (Hellsten et al. 1999), fangueo aquatic tractors (Osland et al. 2011), aquatic weed-wackers (Lishawa et al. 2015), conventional agriculture equipment including haybines and rotary disc mowers (Grosshans et al. 2013; Grosshans et al. 2014; Svedarsky et al. 2016) and a tracked biomass harvester (Lishawa et al. 2017) (Fig. 9d) have been used to remove *Typha* or reduce its biomass. In the PPR, Smith et al. (2016) found that physical removal of *Typha* and the underlying sediment from wetlands resulted in plant communities that were closer in composition and structure to uninvaded reference wetlands. Reducing aboveground biomass by cutting and then flooding was shown to be effective by reducing O_2 transport to the rhizomes and limiting future growth (Weller 1975; Sale and Wetzel 1983; Jordan and Whigham 1988; Ball 1990). Likewise, cutting *Typha* below water and removing its biomass results in high levels of *Typha* mortality (Berke 2017; Lishawa et al. 2017). Where flooding is not possible, cutting *Typha* ramets when stored carbohydrates in the rhizomes are at their lowest concentrations reduces survival (Sojda and Solberg 1993). Multiple cuts may be necessary to draw down robust rhizome carbohydrate reserves; Hall and Zedler (2010) found that four cutting treatments in one season were necessary to reduce *T.* × *glauca* rhizome starch concentrations below reference levels in a nutrient-enriched urban wetland. Additionally, repeat and follow-up treatments such as herbicide application are often needed to reduce new growth from re-sprouting (Wilcox et al. 2018).

Biomass Harvest

Harvesting *Typha* biomass and its litter for bioenergy production consistently increases native biodiversity and habitat complexity over the short-term under a range of environmental conditions. In a heavily invaded Lake Huron coastal wetland, aboveground harvest under dry and flooded conditions in summer resulted in a doubling of native plant species richness and diversity for at least 2 years following treatment (Lishawa et al. 2015; Berke 2017). Lishawa et al. (2017) found that harvesting *Typha* biomass above water appears to be more effective for restoring native emergent plant dominance in younger *Typha* stands, while cutting below water significantly increases subm ergent plant diversity. Harvesting *T. domingensis* biomass in central Mexico increased native species richness and Shannon diversity (Hall et al. 2008). While harvesting alone does not always eliminate *Typha*, it consistently increases native plant diversity; however, repeated harvests are likely needed to alter environmental conditions in invaded stands. Five years after a one-time aboveground *Typha* harvest, no differences were detected between harvested and unmanipulated *Typha*-dominated reference plots in terms of microbial community composition, CO_2 flux, or porewater nutrient concentrations, despite an increase in the relative dominance of native species (Keyport et al. 2019). This suggests that the legacy effects of *Typha* invasion on sediment parameters may be more persistent than those on plant community composition.

Herbivory and Grazing

Herbivores such as muskrats, cattle, goats, and geese will feed on *Typha* seedlings, as well as roots, stems, and leaves of mature plants (Takos 1947; Bellrose 1950; Smith 1988; Lacki et al. 1990; Nelson et al. 1990a; Sojda and Solberg 1993; Campbell and MacArthur 1994; Silliman et al. 2014). The grass carp (*Ctenopharyngodon idella*) has even been identified as a potential control agent for *Typha* (Carney and deNoyelles 1986), although many states prohibit its introduction. Muskrats also favor *Typha* for use in constructing lodges (Bellrose and Brown 1941; Danell 1979; Clark 1994). Although research and observation indicate that muskrats may decrease *Typha* biomass (Sojda and Solberg 1993; Connors et al. 2000; Farrell et al. 2010), formal research assessing the potential of muskrats to control extensive *Typha* stands is limited. Silliman et al. (2014) demonstrated that grazing by goats or other livestock can be an effective method for controlling *P. australis*, suggesting that it may also be a viable control option for *Typha*. Sojda and Solberg (1993) suggested that grazing-associated mortality of mature plants is rare, especially for those with extensive rhizomes, but that grazing could be effective in controlling seedlings. Also, reducing *Typha* litter biomass using invertebrate litter consumers, such as shrimp (Kong et al. 2019), may improve growth of native plants. As with other treatments, effects of grazing likely would be maximal when combined with other treatments (e.g., water-level manipulation), and implementation should consider the life history of *Typha* (Sojda and Solberg 1993).

Re-Vegetation

Plant community composition following *Typha* removal is dependent on the composition of the remnant seed bank, incoming propagules, and environmental conditions (e.g., nutrient regime). Studies have shown that seed banks play an important role in wetland vegetation dynamics and that seed banks and plant species composition of disturbed wetlands can be quite different than those of natural wetlands (van der Valk and Davis 1978; Galatowitsch and van der Valk 1996; Gleason et al. 2003). Therefore, the addition of competitive herbaceous species by planting plugs and/or seeding may be needed to supplement natural recovery of native plant species (Smith et al. 2002; van der Valk and Baalman 2018) (Fig. 9e). Soil transplantation also has shown promise as a technique for establishing desired wetland vegetation while inhibiting the spread of *Typha* (Brown and Bedford 1997). In terms of assessing the success of restoration or re-vegetation efforts, prolonged studies are required since vegetation succession trajectories often do not follow long-term expectations, and hydrologic conditions of wetlands can vary significantly over time (Zedler 2000; Euliss et al. 2004; Aronson and Galatowitsch 2008; Matthews et al. 2009; Matthews and Spyreas 2010).

Nutrient Management

Typha response to nutrient enrichment is stronger than that of many competing species (Newman et al. 1996; Woo and Zedler 2002), suggesting that *Typha* management could be more effective if combined with nutrient reductions (i.e., treating an underlying cause of *Typha* dominance). In a modeling study, Elgersma et al. (2017) found that reducing nutrient inputs was more effective at limiting *Typha* growth compared to herbicide, fire, or mowing in the absence of nutrient reductions. A small-scale experimental study using C additions to sequester N demonstrated that reductions in nutrient availability can reduce the competitive ability of a nitrophilic wetland invader (Perry et al. 2004), but large-scale application of this approach is logistically challenging, especially in wetlands. When restoring degraded or former cropland wetlands, methods also include excavation of accumulated sediments and associated biomass such as *Typha* rhizomes that will also remove nutrients from the wetland (Smith et al. 2016) (Fig. 9f). Watershed-scale nutrient reduction efforts are extremely challenging to implement, especially given the predominance of nonpoint sources of nutrients in agricultural areas where *Typha* invades, such as the LGL, Lake Winnipeg watershed, Everglades, and PPR (Luscz et al. 2015). Observed declines in *Typha* expansion during a period of reduced external nutrient loading in the Everglades (Rutchey et al. 2008) provides some evidence that nutrient reductions may indirectly benefit management efforts. Recent large-scale studies indicate that external nutrient-load reductions, combined with active *Typha* management, can result in the establishment of more desirable emergent and submerged species, which in turn can reduce nutrient accumulation (Newman et al. 2018) and potentially *Typha* regrowth.

Management Trade-Offs

Ultimately, managing *Typha* involves trade-offs. While cutting followed by flooding or cutting below water is highly effective at killing *Typha* (Weller 1975; Sale and Wetzel 1983; Jordan and Whigham 1988; Ball 1990), this approach results in high levels of mortality to native emergent species as well (Lishawa et al. 2017). Amphibians and other gill-breathing organisms are also at risk from aggressive and high frequency nature of *Typha* control, particularly during early spring and summer when larvae are present and metamorphosing, although there is still considerable uncertainty regarding these impacts (Krynak et al. 2017).

In the Everglades, initial active *Typha* management efforts using aerially applied glyphosate and imazapyr shifted a *Typha* marsh to an open water habitat dominated by periphyton and submersed aquatic-vegetation, but it also removed remnant macrophytic vegetation typical of Everglades marsh communities (Hagerthey et al. 2014). However, the use of herbicide for selective *Typha* control may provide opportunities to limit mortality to remnant native-plant communities targeted for restoration and may present a viable management option when mechanical removal techniques are impractical. Rodgers and Black (2012) found that aerial applications of imazamox at moderate doses effectively controlled *Typha* for 1 year in Everglades marsh plant communities, with little to no mortality of other native plant species. By contrast, aerial imazamox applications in highly nutrient enriched areas with greater *Typha* densities resulted in moderate *Typha* control and required follow up treatments to sustain control (Newman et al. 2017; Newman et al. 2018). However, regular use of herbicides may also lead to herbicide resistance and spread of more resistant hybrids (Zheng et al. 2017). Thus, additional research on selective control of *Typha* is needed to determine species-level differences among *Typha* congeners and the tolerance of other wetland species to lower imazamox application rates in order to minimize frequency and rates of application.

Integrated *Typha* management strategies, which emphasize a holistic approach by utilizing combinations of control methods, may improve *Typha* management outcomes while reducing the reliance on herbicides (Buhler 2002; Buckley et al. 2004). Which combinations and sequencing of management tools will be most effective is likely dependent on the species of *Typha*, environmental conditions, management objectives, and scale of management operation.

Section 6: Future Research Needs

Despite the abundance of research articles on *Typha*, there are still major research gaps that need to be addressed. Here we identify several essential topics for future research.

Distribution

Niche modeling approaches are needed to better predict future distributions of all *Typha* taxa under scenarios of global change, as there have been few studies on climatic limitations of *Typha*. Scenarios to be explored through modeling should focus on the role of warmer temperatures and changes in timing of seasonal temperature shifts, magnitude of annual and diurnal temperature ranges, and frequency of extreme temperature maxima or minima. Modeling efforts should also include exploring the effects of altered hydrological regimes, other human impacts, including eutrophication and road salt inputs (Hood 2013), competing invasive species (e.g., *P. australis*), and the direct effects of higher CO_2 on *Typha* distributions.

To validate resulting models, paleoecological records extending through Pleistocene interglacials and pre-Quaternary intervals, particularly those that experienced warmer temperatures than the Holocene and are potential analogs for future warmer worlds (Fischer et al. 2018), are needed. These will inform constraints on future distributions of *T. angustifolia* and other *Typha* species. *Typha* pollen and macrofossils are documented in paleobotanical records at least as old as the early Miocene (23 million years ago) (Lee et al. 2012), suggesting that the fossil record can be further exploited to understand the responses of *Typha* to global change.

Genetics

Future work is urgently needed on the potential contributions of non-native lineages to regional patterns of invasion by *Typha* in North America. Recent work by Travis and Marburger (unpublished data) using microsatellite markers indicated the possibility of introgression of *T. angustifolia* alleles into northern Everglades *Typha* populations, in spite of the apparent absence of pure *T. angustifolia* in the region. This observation is explainable through linkage of microsatellite markers to *T. angustifolia* genes under positive selection, whose spread well ahead of the actual hybridization front could have been facilitated through a pattern of repeated backcrossing to increasingly southern populations of either *T. domingensis* or *T. latifolia*. Note, however, that firm conclusions in this regard await a more thorough characterization of *T. domingensis* alleles, which may partially overlap with those of *T. angustifolia*.

Additionally, evidence for tri-hybrid crosses among the three *Typha* species needs further exploration. Development of more nuclear and cytoplasmic markers, as well as whole genome sequencing, could clarify genetic relationships of the species and hybrids, while seed bank/pollen studies across North America would show the regional variation and persistence of hybrids over longer periods of time.

Ecological Impacts

The majority of research on the ecological impacts of invasive *Typha* has focused on changes in plant and avian communities. However, *Typha* invasion impacts all wetland trophic levels, and more research on the impacts of *Typha* on fishes, invertebrates, amphibians, and pollinators is needed. Studies should examine the potential impacts of *Typha* invasion on wetland food webs, as well as on the makeup and structure of wetland biotic communities (e.g., aquatic invertebrates, amphibians). In the PPR, research related to pollinator habitats, including wetlands, has been identified as nationally important. Focal areas for research should include impacted areas such as the LGL, Florida Everglades, and PPR, along with areas that are likely to be impacted.

Biogeochemistry

Soils in *Typha*-dominated wetlands tend to have greater rates of denitrification, as well as N mineralization. However, to the best of our knowledge, a comprehensive N-budget that directly compares these elevated rates of N mineralization against increased denitrification rates is not yet available. A related question with management implications is how to reverse the positive feedback between nutrient availability and *Typha* species invasions. Further, experimental investigation of how *Typha* invasion alters rhizospheric-microbial relationships and CH_4 emissions is necessary to better understand the role of *Typha* invasions on wetland C balance.

Management

The initial question regarding *Typha* management relates to the decision on when it is necessary. Some obvious cases for management are in natural areas where native vegetation has been displaced by *Typha* invasion, mostly by *T. angustifolia* and *T.* × *glauca* (e.g., Wilcox 1986; Wilcox et al. 2008) or when the native *Typha* species, e.g., *T. domingensis* has created a monoculture due to anthropogenic disturbance (Newman et al. 1998; Smith and Newman 2001). However, in other cases, especially when *T. latifolia* is the *Typha* species present, photointerpretation studies may be needed making use of historical imagery to determine if invasion is ongoing. Models constructed in a GIS environment may be developed to predict future changes in *Typha* invasion and need for management, such as when changes will be made in water-level management (e.g., Wilcox and Xie 2007). There is also a very real need for information on when it is necessary to repeat management. The effects of *Typha* management are often temporary, but the extent to which this is the case is often hard to know because of the lack of long-term monitoring in most restoration projects.

An interdisciplinary, systems approach is needed for *Typha* management, especially for *T.* × *glauca*; ideally *Typha*-choked wetland basins could be partially harvested to achieve a spectrum of uses, including enhanced wildlife habitat, nutrient bioremediation, biofuel production, bioproduct generation (e.g., construction materials), stimulation of local economies, and climate change mitigation. Simultaneous research is needed to identify the appropriate combination of biological, engineering, and economic conditions of various sites needed to achieve project feasibility. A major outstanding question is why *T.* × *glauca* is so problematic from a management perspective in so many places, whereas *T. latifolia* is present in these regions but is generally not a management concern. Little is known about the role herbivores and pathogens play in limiting growth of different *Typha* taxa, and whether 'enemy escape' plays a role in *Typha* invasions. Better understanding these questions using basic ecological research will promote systems-based management approaches. A complementary approach might include an economic Input-Output model integrating the costs and benefits of *Typha* management in relation to biomass harvest and agriculture damage (Shwiff et al. 2017). Finally, there is great potential to improve management and stewardship responses to *Typha* invasions through collaboration with indigenous peoples to integrate customary and traditional uses of *Typha* by local communities.

Despite frequent mention of integrated pest management (IPM) as a cost-effective, environmentally-sound approach to invasive plant management, there is little research involving *Typha* and IPM (but see Mallik and Wein 1986; Kostecke et al. 2004; Wilcox et al. 2018). More research is needed to determine optimal combinations and sequencing of control tools for *Typha*, particularly in systems where *Typha* is often difficult to control. For example, sustained control of *T. domingensis* is challenging in nutrient-enriched Everglades marshes using herbicides or fire alone (Newman et al. 2018). In addition, tradeoffs between *Typha* management and downstream impacts of *Typha* management, e.g., translocation of nutrients to unenriched areas, require further investigation. Field studies evaluating different control tool combinations may reveal sustainable management strategies. However, it is important to note that IPM strategies are likely to be highly influenced by scale, as well as species- and region-dependent given documented variation in management outcomes. Therefore, studies should encompass a broad range of habitats such as the LGL, Florida Everglades, and PPR, be conducted at appropriate scales to inform management (e.g., management unit, wetland complex), and be of adequate length to assess long-term outcomes.

Acknowledgments This research was funded in part by the U.S. Geological Survey Land Resources Mission Area, Land Change Science Research and Development Program. We sincerely thank the many scientists who have contributed to our understanding of *Typha* through decades of dedicated research on this genus. We thank Jacob Meier and Olivia Johnson for assistance with figures, Lowell Washburn and Craig Bihrle for deer and pike photos, and Isa Woo and Gregg Knutsen for reviewing our manuscript.

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